G.S. Hochbaum
C.J. Walters

Components of hunting mortality in ducks

Environment Canada
Environnement Canada

Canadian Wildlife Service
Service canadien de la faune

G.S. Hochbaum*
C.J. Walters†

Components of hunting mortality in ducks: A management analysis

Occasional Paper
Number 52
Canadian Wildlife Service

Également disponible en français

*CWS, Winnipeg, Manitoba R3T 2N6

†Institute of Animal Resource Ecology,
University of British Columbia,
Vancouver, B.C. V6T 1W5

Issued under the authority of the
Minister of the Environment
Canadian Wildlife Service

©Minister of Supply and Services Canada 1984
Catalogue No. CW69-1/52E
ISBN 0-662-13036-7
ISSN-0576-6370

Design: Rolf Harder & Assoc.

Contents

4	Acknowledgements
5	**Abstract**
5	**Introduction and conceptual model**
6	1. Interactions and components
7	2. Hypotheses
8	**Study areas, hunting regulations, and methods**
8	1. The Delta Marsh
9	2. The Pasquia Marsh
9	3. Decoy trials
9	4. Aerial surveys
10	5. Spy blinds and hunter effort
11	**Field results**
11	1. Vulnerability
13	2. Hunter selectivity and observed kill
14	3. Handling time
14	4. Relation of flock size to probability of mortality
16	5. Density–kill relationship
16	6. Analysis of hunter bag data
17	7. Allocation of hunter effort
17	8. Crippling losses
17	**Discussion**
20	**Mathematical model for a single hunter**
20	1. Background to the model
20	2. Quantifying the model
22	**Management analysis and implications**
22	1. Applying the model to the Delta Marsh
22	2. Results and discussion
24	3. Management implications of findings
26	**Summary and conclusions**
27	**Literature cited**

List of tables

12	Table 1. Results of 36.8 h of decoy trials during the 1973 field season
12	Table 2. Results of 45.6 h of decoy trials during the 1974 field season
13	Table 3. Proportion of ducks using refuges on the Delta Marsh during October, as measured by aerial surveys during 1973
13	Table 4. Summary of *F* ratios generated by regression analysis of vulnerability as related to selected weather variables
13	Table 5. Hunter selectivity by species as determined by observation on the Delta Marsh during 1973, 1974, and 1977
14	Table 6. Observed kill, kill per hunter-hour, estimated effort, and population size for the Delta Marsh in 1973 and 1974
14	Table 7. Hunter success on the Delta Marsh as determined by hunter bag checks during 1973–1977
14	Table 8. Probability of being killed or wounded in relation to range from hunters' blinds on the Delta Marsh (1973, 1974)
15	Table 9. Calculations of probability of one hunter killing a bird showing adjustment for flock sizes and hunters
15	Table 10. Mean flock sizes of ducks lured to decoys and probability of mortality based on flock size
16	Table 11. Estimated kill, population size, and hunter numbers at Delta for selected weeks during 1975, 1976, and 1977
16	Table 12. Crippling losses in relation to range from hunters' blinds on the Delta Marsh (1973, 1974, 1977)
18	Table 13. Possible influences of independent variables on the kill of ducks as predicted by three models

List of figures

6	Figure 1. Conceptual model of duck–hunter interactions assumed to represent causal factors determining the kill for one hunter
11	Figure 2. Duck populations of the Delta Marsh during the falls of 1973–77 as determined by aerial surveys
11	Figure 3. Estimated hunter-hours during each week of hunting during 1973 and 1974 and estimated numbers of hunters during each week of hunting in 1975, 1976, and 1977
15	Figure 4. (*a*) Probability of death in relation to flock size as determined from spy blinds on the Delta Marsh during 1973 and 1974 and (*b*) relationship between probability of death and flock size as determined from spy blinds on the Delta Marsh during 1973 and 1974

20	Figure 5. Functional relationship between potential kill per hunter-hour and duck density
23	Figure 6. Isopleth diagram showing the relationship between regions of Mallard kill and population size and season length under normal effort levels observed at Delta
24	Figure 7. Isopleth diagram showing the relationship between regions of Lesser Scaup kill and population size and season length under normal effort levels observed at Delta
25	Figure 8. Isopleth diagram showing the relationship between regions of Canvasback kill and population size and season length under normal effort levels observed at Delta

Acknowledgements

We are grateful to all of the people who contributed to this project.

We are particularly indebted to Conrad Wehrahan. We would like to thank the late Douglas Stephen of the Canadian Wildlife Service (CWS) for partially funding the study. Kent Brace and James Patterson, CWS, allowed time to continue the project. Dale Caswell, CWS, gave statistical and programming advice. We also thank Hugh Boyd, CWS, for his editorial advice.

We wish to thank Robert Jones, Bruce Batt, and Peter Ward of the Delta Waterfowl Research Station for financial support, advice, and encouragement. Monies were also contributed by the Canadian National Sportsman's Show. The Bell Estate permitted use of their landings, boats, and decoys, and the guides of St. Ambroise gave frequent advice. Louis Ducharme Sr., chief guide of the Bell Estate, shared many thoughts on the natural history of ducks and sport hunting in general. We are also indebted to the three assistants, Richard Wishart, Kevin Ward, and Valerie Hochbaum, for their help and endurance, especially on those mornings in October when the wind was up and the temperature below freezing.

Abstract

This study was conducted to evaluate waterfowl hunting and kill on the Delta Marsh, Manitoba, using a modified predator–prey model, by monitoring the numbers and behaviour of ducks and hunters. Twelve hypotheses were formulated to test the following: the vulnerability of different species in relation to hunter effort, determinants of bag size, determinants of hunter effort, effects of weather on kill, and whether or not hunters were selective. Aerial surveys and experimental hunts were conducted and kill statistics gathered on the Pasquia and Delta marshes in Manitoba to evaluate predictions from the hypotheses.

Field data showed that duck vulnerability is inversely proportional to hunting effort and that ducks are most wary when hunter effort is greatest. Hunters were most numerous when duck densities were high. Hunters did not shoot selectively and crippling losses approximated one-third of the birds shot. Weather had little influence on the kill. Distribution patterns of ducks were clumped. The probability of mortality for an individual duck decreased with increasing flock size. Handling time per bird downed did not limit bag sizes. Time between encounters was independent of duck numbers. The relationship between kill and duck density was non-linear.

Simulation tests of various management schemes revealed that harvests of Mallard and Lesser Scaup would not be greatly affected by increased hunter effort, and that season length and population size strongly influence harvest. Shortened seasons are recommended if reductions in the kill of Mallard are thought to be required. Lesser Scaup require no special regulations. Open season on Canvasbacks should only occur when local numbers exceed 5000 and should be less than 2 weeks.

The predator–prey model is recommended for analysis of local regulations. Multivariate statistical models may be more useful in forecasting yields on a regional level.

Introduction and conceptual model

Few attempts have been made to apply our knowledge of predation in animal populations to predation by humans. Holling (1959 *a*, 1966) in his pioneering work on the functional response of predators to varying prey densities, developed models to describe capture rates. Walters *et al.* (1973) applied those equations to data from field studies in southwestern British Columbia, and stated that, for such models to be useful in waterfowl management, further research was needed on the basic components, particularly avoidance learning by ducks.

Several researchers have attempted to forecast long-term waterfowl yields using population dynamics models. Geis *et al.* (1969) employed a multiple regression model for estimating allowable harvests of Mallards in the US. Walters *et al.* (1974) incorporated numerous biological relationships into a continental Mallard model but found the forecasts of little value because many variables and parameters could not be estimated. More recently, Anderson (1975) and Brown *et al.* (1976) have attempted to predict Mallard harvests for North America by using rough estimates of total pond numbers (the US Fish and Wildlife Services pond index) and an extension of the Beverton and Holt (1957) stock-recruitment equation. Hochbaum and Caswell (1978) created individual mathematical models of federal management programs for Mallards for each of the western provinces, and Cowardin and Johnson (1979) evaluated management programs for local areas in the north-central US. None of those models deals with the behavioural interactions of hunters and ducks that determine, at the local level, the effectiveness of regulatory actions (such as variations of season length and bag limits) employed to achieve allowable long-term harvests. Further, they ignore the multi-species character of waterfowl harvesting; seldom can regulations be tailored to fit all the species that hunters may pursue simultaneously.

Throughout North America, duck hunting regulations seem to be based on the assumption that all species are equally vulnerable to gunning; policy is based primarily on stock size. However, most hunters are aware that hunters' opportunities for taking ducks vary according to many factors, including species present, location, and time of season. Some variation in vulnerability may be due to specific avoidance behaviour learned by the birds (Walters *et al.* 1973).

Our objectives were (1) to determine how waterfowl and hunters interact within a hunting season and how this interaction affects the kill; (2) to incorporate our field data into a multi-species predator–prey model; and (3) to explore the management implications of our findings. To meet these objectives we took field measurements of the interactions between single hunters and several species of ducks and applied them in simulation models to determine the effective-

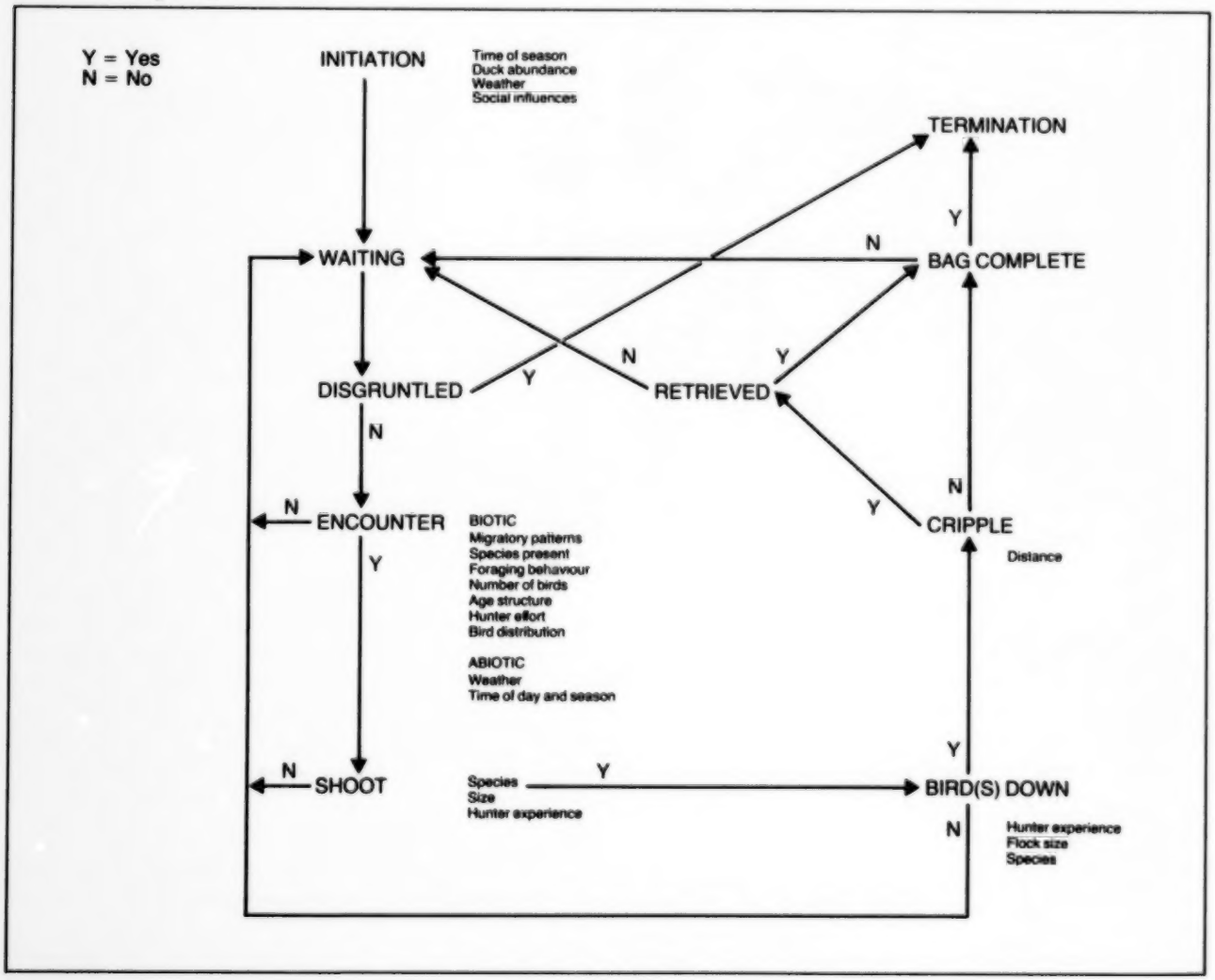
ness of regulations. The study involved three phases. First, we developed a conceptual hunting model based on the components that determine a hunter's kill; we used the model to develop specific hypotheses that could be tested in the field. Second, we studied duck–hunter relationships in the Delta Marsh in south-central Manitoba during 1973–1977, and Pasquia Marsh in north-central Manitoba in 1974. The two marshes were ideal study areas: they have large populations of ducks during the fall and are favoured hunting areas. Finally, we developed a within-season model that provides a general analysis of our findings and helps managers forecast the effects of duck-hunting regulations on an annual basis.

1. Interactions and components

An ideal study of ducks and hunters would involve large-scale, controlled comparisons of daily kill with the bird density and hunter effort on that day. Such experiments, being labour-intensive and requiring the informal co-operation of many hunters, are not considered practical by regulatory agencies. Because hunting effort was uncontrolled and varied in patterns that did not necessarily provide appropriate experimental contrasts, we were obliged to construct a model from a study of the factors influencing the success of the hunt. First, we looked at how a single hunter acts when pursuing ducks in a marsh. We created a conceptual duck-hunting model that shows the causal pathways connecting the hunter's actions (Fig. 1). According to this model, initiation of the hunt depends on duck abundance, date, weather, and various social influences. Once in the marsh, the hunter places decoys, then hides nearby in a blind. When ducks approach the decoys, the hunter must decide whether or not to shoot. If the hunter fires, a bird may be killed and brought to bag or, only crippled, the quarry may try to escape. The hunter may then seek to kill and bag the cripple. When the hunter has taken the maximum number of dead ducks allowed by law, (the daily bag limit), the hunt should end. Of course, a hunter may lose interest for lack of birds or extreme cold and abandon the hunt before reaching the permitted total kill.

Within the model the rate of encounters during the hunt is used as a measure of the opportunity to kill ducks (Fig. 1). Encounter rates reflect vulnerability and may be affected by several variables: foraging and migration behaviour, hunter effort, number of birds present, species composition, age structure of flocks, bird distribution in relation

Figure 1
Conceptual model of duck–hunter interactions assumed to represent causal factors determining the kill for one hunter



to hunters, local weather, time of day, and season. Several other components influence the outcome of each encounter. The hunter's decision to shoot may be related to species, size of the bird, and the hunter's experience. Selectivity influences the size and composition of the daily bag. No hunters kill ducks in every encounter, success depending on the accuracy of the gunner, range of the ducks, flock size, and species. Crippling losses affect the kill because birds not retrieved are not included in the bag; handling time spent pursuing cripples is not available for shooting other ducks that pass by. Some hunters do not pursue cripples lest they lose opportunities to shoot at passing ducks, including those attracted by their decoys.

Figure 1 shows how the relationship between duck density and the rate of hunter–bird encounters ultimately determines how many birds will be fired upon and killed during times when the hunter is ready to shoot.

In many countries and for hundreds of years, hunters have used decoys to exploit the flocking behaviour of ducks. Encounter rate per duck depends on bird movements and response to the lure of the hunter's decoys. Encounter rates will decrease if (1) birds move less, or restrict their movements to areas where decoys are not present, or (2) birds become more wary or less attracted to groups of decoys or live ducks.

Waterfowl are gregarious except during the breeding season. Flocking facilitates pair formation during the fall and winter (McKinney 1975), enhances foraging efficiency (Bailey and Batt 1974), aids in predator detection (Powell 1974, Seigfried and Underhill 1975), and brings birds to common shelter during wind and storm. Immature birds which have not previously visited the winter grounds join flocks of experienced adults in fall migration (Hochbaum 1955).

2. Hypotheses

Figure 1 identifies the basic relationships that could influence harvest, but it says little about the quantitative nature or relative importance of each. Walters *et al.* (1973) suggest, for example, that observed kill patterns in southern British Columbia cannot be explained by duck abundance and handling time alone. They believe that avoidance learning by ducks has an important influence on hunter success, and that most hunting regulations have little impact on the kill at local level. We attempted to identify major uncertainties and interactions suggested by the model and to express these as a series of 12 hypotheses to be tested in the field:

H1. Ducks learn to recognize the danger of hunters' blinds and decoys through experience. One prediction testing this hypothesis is that vulnerability (defined as the likelihood of a duck encountering and being killed by a hunter) will decline as cumulative hunting effort increases through a hunting season. Thus, by November, birds are wary and have modified their behaviour to avoid (*a*) specific objects such as blinds and decoys, or (*b*) hunted areas in general.

H2. The behaviour of ducks towards hunters is species-specific. Avoidance of hunters changes in different ways for different species during the hunting season.

H3. Encounters between hunters and ducks take place at random but the rate of encounter per hunter is related to population size: kill and encounters increase linearly with duck abundance.

H3C. A counter hypothesis is that bird distribution is highly clumped and that hunters search non-randomly so that they have effective access to the same number of ducks over a wide range of population sizes.

H4. Handling time per bird shot or crippled effectively limits the daily bag except at very low bird densities.

H4C. Alternatively, handling times are short enough so that either encounter rates or management bag limits determine bag per hunter.

H5. Hunter effort is determined by the numbers of ducks present and time of the hunting season. We predicted that effort would be greatest early in the season when ducks are most numerous.

H5C. A counter hypothesis is that hunting patterns are established through tradition and will not respond quickly to changes in bird density.

H6. Vulnerability is related to local weather conditions. We predicted that avoidance behaviour would be influenced by prevailing weather. For example, most hunters believe that duck hunting is best when it is overcast and windy. Therefore, high vulnerability might be related to weather patterns measured by changes in barometric pressure, temperature, air movement, and relative humidity.

H6C. An alternative hypothesis is that kill patterns are not influenced by local weather.

H7. Hunters shoot discriminately and as a result they forego the opportunity to kill some species of ducks.

H7C. A counter hypothesis is that hunters shoot at anything that flies past.

In addition to testing these 12 hypotheses, we hoped to gain a better understanding of the influence of age of the bird on the kill and also to determine crippling losses by direct observation. Studies (e.g., Bellrose *et al.* 1961) have shown juveniles to be more vulnerable to gunning than older ducks. Sowls (1955) found hunters' reports of crippling losses to be curiously high on the Delta Marsh.

The following terms are used repeatedly in the text.

Avoidance learning: any alteration in the behaviour of individual ducks as the result of experience that reduces the likelihood of being killed by a hunter.

Crippling loss: a measure of the number of ducks that are hit by gunfire, not immediately killed, and not retrieved. Birds in this category are often referred to as "sailers." The loss is calculated as the ratio of crippled birds to the number of birds downed by hunters.

Decoy trials: observation periods during which the investigator simulates a hunting situation using a blind and decoys. The technique is employed to measure the degree of avoidance learning. Birds that respond to the decoys are negatively reinforced by gunfire.

Encounter rate: the number of each species observed per hour within 35 m of a blind during a decoy trial.

Flare: an avoidance behaviour elicited when ducks detect a hunter. In flaring, the birds turn quickly in the air and fly away from the gunner thus presenting a difficult target.

Handling time: the amount of time a hunter spends for each encounter in activities other than effective search and shooting. This includes time spent reloading the gun and retrieving downed birds. This time, which could not be measured directly, is estimated by subtracting mean time between encounters when birds are fired upon (unsuccessfully) from mean time between successful encounters (birds killed) and the next encounter.

Hunter effort: an index of the hours hunted per week, calculated by dividing the weekly kill (as determined by bag checks) by the number of ducks bagged per hunter hour during spy blind observations.

Hunter encounter: duck or ducks estimated by the observer to be passing within killing range (35 m) of a hunter, whether shot at or not.

Killing range: the maximum distance at which ducks can be killed consistently with a 12-gauge shotgun. This distance was estimated at 35 m by Bellrose (1953). We used this statistic in calculations of encounter rates and hunter selectivity.

Maximum kill: the maximum number of ducks killed per hunter hour.

Probability of kill: the ratio of ducks downed to ducks fired upon.

Selectivity: the percentage, by species, of ducks fired upon in hunter encounters: [(shots at species X) / (encounters with species X)] × 100.

Spy blind: a simulated hunter's blind, from which the investigator observes gunners.

Vulnerability coefficient: an index of opportunity to kill ducks as measured by the mean weekly encounter rate per hour for a species divided by its estimated population size for that week. The coefficient represents the risk per hour of a bird in the population encountering a hunter and is the rate of effective search of Holling (1959*a*). This coefficient is not to be confused with the (relative) vulnerability quotient used by Bellrose *et al.* (1961) as a measure of the greater likelihood of young ducks and geese being killed, as a result of inexperience in comparison to the susceptibility of older ducks.

Study areas, hunting regulations, and methods

1. The Delta Marsh

The Delta Marsh, along the south shore of Lake Manitoba, is one of the major waterfowl harvest areas on the Canadian prairies. A narrow ridge of sand covered with poplar (*Populus* spp.), ash (*Fraxinus* sp.), maple (*Acer negundo*), and willow (*Salix* spp.) separates the 20 235 ha of marshland from the lake. To the south of the wooded ridge lie vast stands of reed grass (*Phragmites communis*) broken by large open bays bordered with bulrush (*Scirpus* spp.) and cattail (*Typha* spp.). The marsh is joined to the lake by five channels allowing its water levels to fluctuate with wind tides on the lake. Reed grass is separated from upland borders by extensive meadows of whitetop grass (*Schlochloa festucacea*). On drier areas, some of which are hayed and grazed, the whitetop is interspersed with sow thistle (*Sonchus arvensis*), aster (*Aster* sp.), foxtail (*Hordeum jubatum*), and goosefoot (*Chenopodeum rubrum*).

Many spring migrants, primarily Mallard (*Anas platyrhynchos*), Pintail (*Anas acuta*), Canvasback (*Aythya valisineria*), Redhead (*Aythya americana*), Lesser Scaup (*Aythya affinnis*), Blue-winged Teal (*Anas discors*), Wigeon (*Anas americana*), Shoveler (*Spatula clypeata*), and Gadwall (*Anas strepera*) stop at the Delta Marsh in April. Some remain to nest; others journey on to nesting grounds in north-western Canada. The large open bays of the Delta Marsh, with their emergent and submergent aquatic plants, continue to serve as a major moulting range for dabbling ducks which are numerous there during the flightless period (mid June – mid August). Diving ducks prefer to moult on several large lakes in west-central Manitoba. Both dabblers and divers gather subsequently at Delta, an important staging area from late August through October. Adult Mallard and Pintail are on the wing by early August, their numbers bolstered by young of the year. After mid August, these two species commonly associate in morning and evening flights from marsh to adjacent stubble fields. Mallards remain common until freeze-up in late October or early November; most Pintail have migrated by mid September. A build-up of Blue-winged Teal on the sloughs and creeks of the marsh occurs in August, most departing by the end of September. Canvasbacks and Redheads, mostly young of the year and adult females, arrive about 1 September and depart in mid October. Lesser Scaup are common on the open bays until the end of October, with smaller numbers of Bufflehead (*Bucephala albeola*) and Green-winged Teal (*Anas crecca carolinensis*).

Hunting on the eastern portion of the Delta Marsh, site of our studies, opened on 8 October 1973 and 7 October 1974. The legal close of shooting was 1 December 1973 and 30 November 1974. In both years, the gunning ceased when

the marsh froze over by 7 November. During both years the daily bag limit was six ducks, modified by special regulations for some species. In 1973 and 1974 only one Canvasback or one Redhead could be taken daily while Mallard kill was restricted to three per day in 1973, two per day in 1974. In Manitoba as a whole, two additional Lesser Scaup were allowed as "bonus" ducks after 8 October in 1973, but this extra allowance did not hold the following year.

In 1975, 1976, and 1977 the legal limits were six, eight, and six ducks per day, respectively, to include no more than three Mallards daily and either one Canvasback or Redhead. Hunting began 6 October 1975, 27 September 1976, and 8 October 1977 and ended at freeze-up during the second week of November in all 3 years.

2. The Pasquia Marsh

The 1820-ha Pasquia Marsh is located in northern Manitoba about 32 km southwest of The Pas. Drainage ditches link the 65 ha of open water in the centre of the marsh with a channel leading into The Pas River. The outer borders of Pasquia Marsh are dominated by stands of willow, cord grass (*Spartina* spp.), and reed grass. The heart of the marsh holds islands of cattail and hardstem bulrush (*Scirpus acutus*), with water milfoil (*Myriophyllum* spp.) the common submergent.

Pasquia Marsh, bordered on the north and west by agricultural land, is a favoured staging area for field-feeding Mallard and Pintail in August and September. The marsh is used infrequently by diving ducks, which prefer the larger lakes in The Pas region with their dense beds of sago pondweed (*Potamogeton pectinatus*).

In 1974, the Pasquia Marsh opened to hunting on 9 September and closed on 30 November. Daily bag limits and restrictions were the same as those on the Delta Marsh: six ducks, including no more than two Mallards and one Canvasback or Redhead.

This area was studied in 1974 only, to contrast vulnerability with Delta. All the birds left the marsh 5 days after hunting began so that a full comparison was impossible.

Although we could not test 12 hypotheses by direct manipulation of birds and hunters, we knew that natural situations produce radical changes in these variables through each hunting season, so that appropriate monitoring would provide some of the necessary contrasts. Our field studies had the following objectives:

1. To gather information on the vulnerability of ducks according to their species, age, and experience with hunters, and in different kinds of weather;

2. To estimate numbers and species of ducks on the study areas and monitor their behaviour during the fall; and

3. To measure hunter effort and observe hunter behaviour (cripple rate, selectivity, handling time), at different times during the season.

3. Decoy trials

We used decoy trials to evaluate the effects of hunter density, waterfowl species composition and age, and weather on vulnerability. Teplov and Kartashev (1957), Olson (1965), Stott and Olson (1972), and Alford and Bolen (1977), have also used this technique.

Our decoy trials began 1 week before hunting each year and continued until freeze-up during 1973 and 1974. We used 30 decoys in our trials. At Delta, there were 10 each of Canvasback, Mallard, and Lesser Scaup, the most commonly killed species. At Pasquia Marsh we used only Mallard decoys, Mallard being the only abundant duck staging there. Our observation blinds were always on public shooting grounds, in sheltered bays or on the leeward sides of points, sites normally used by feeding and loafing ducks. When ducks responded to our decoys, one of us fired to prevent the birds habituating to the decoys. We observed hunters and ducks when they were most active, from sunrise until 09:00 CST and from 15:00 CST to sunset. From sunrise until sunset, light was sufficient for accurate identification of ducks. At the start of each decoy trial we measured cloud cover and wind speed. We also recorded barometric pressure and relative humidity each day, usually at 06:00 and 17:00 CST to determine their effects on vulnerability. During decoy trials, we kept records of the time of each encounter, the species and number of birds in each flock, and the approximate minimum range of birds from the blind. We set out the decoys at known distances from the blind to facilitate range estimates.

A coefficient of vulnerability for each species was determined weekly during the study from these experimental hunts, by dividing the number of potential kills per hour (number of the birds approaching within 35 m) for each species, by the total number of that species on the marsh. Although the killing range of a shotgun may be greater than 35 m, we selected this as the vulnerable distance since a duck centered in the pattern up to 35 m can be bagged consistently (Bellrose 1953). For example, if 80 Mallard passed within 35 m of my blind during 20 h of observations the rate of encounter was 4 birds per hour. If there were 1000 Mallard in the study area during that period, the vulnerability coefficient would be 4 divided by 1000 or 0.004. The index represents the risk per hour of a bird in a given population passing within gun range of a blind, and is species-specific. Our model suggests that vulnerability may change according to location, time of season, hunting effort, avoidance learning, and flocking behaviour. Vulnerability is also related to sex in the Canvasback and Pintail (Olson 1965, Alford and Bolen 1977) and to the age structure of the population (Bellrose *et al.* 1961). We did not attempt to measure differences in the responses of males and females to our decoys, because juveniles often cannot be distinguished reliably in such circumstances. Ratios of juveniles to adults in the harvest were determined by examination of hunters' bags and used to evaluate differences in vulnerability related to age. We collected these data weekly on the Delta marsh and on opening day at Pasquia Marsh in 1974.

4. Aerial surveys

Each week on the Delta Marsh staff of the Delta Waterfowl Research Station flew aerial surveys and provided estimates of population size and species composition on our study areas. The flights followed east-west section lines at an altitude of 30.0 m, beginning at 09:00 CST after ducks had returned from feeding in stubble fields. Only birds within 0.20 km of the observer's side of the aircraft were counted. These counts were extrapolated to provide an estimate for the entire marsh.

When species identification was not possible, ducks were recorded simply as dabblers or divers. Specific estimates were adjusted if necessary for unidentified birds by the following formula:

$$X = \frac{S}{P}$$

$$Y = X \cdot R, \text{ and}$$

$$T = Y + S$$

where: X = ratio of identified ducks of one species (S) to total identified only as dabblers or divers (P)
Y = species corrected from unidentified category
R = total unidentified dabblers or divers
T = adjusted individual species estimate

In addition to weekly population counts, the staff made four surveys in 1973 to determine distribution patterns of ducks on the Delta Marsh. They flew six transects covering both shooting grounds and refuges, recorded on maps the location of all ducks observed, and calculated the percentage of total ducks using refuges. They flew these surveys at 09:00 CST at an altitude of 100 m.

We made aerial surveys over the Pasquia Marsh on the 3rd day before hunting and on the 3rd and 6th day of the open season. The entire marsh was surveyed, resulting in a complete count.

5. Spy blinds and hunter effort

Because experimental hunts may not be typical, we also (1) monitored other hunters from spy blinds, and (2) analysed the total data on effort and kills collected on the Delta Marsh during 1975–77. We observed and evaluated kills from spy blinds located about 90 m from hunters who showed no evidence of being aware they were under observation. Our blinds and decoy set-ups were authentic and Walters fired his gun now and again as if hunting. We made all observations on public shooting grounds. At peaks, as during opening week and on holidays, we could see three hunting blinds from our hide. More often, only one party was in view. We watched the entire hunt of each group as often as weather permitted. We observed 179 hunter-hours in 8 weeks spread over three hunting seasons.

We recorded the fate of all ducks estimated to be within killing range (35 m) of hunters and all encounters in which birds beyond this range were fired upon. We used these records to determine hunter selectivity.

For each observation period we recorded species encountered, time, flock size, distance of birds from guns, number of birds brought to bag, and the crippling loss, calculated by dividing the number crippled by the number of birds killed and crippled.

With the assistance of Delta Waterfowl Research Station personnel, we conducted a survey of ducks in hunters' bags on the Delta Marsh during 1973 and 1974. We also collected wings weekly at private and commercial hunting lodges. Each week we determined an index for hunter effort by dividing the number of ducks in the bag by the number retrieved per hunter-hour as observed from the spy blinds. The index represents hunter effort in terms of hunter-hours.

In 1975, 1976, and 1977 the Manitoba government monitored hunter effort and duck kill on the Delta Marsh, employing aerial surveys and a bag check. They flew three surveys a week and estimated numbers of hunters by counting hunting parties and multiplying by average party size. Flights began at 08:00 CST at an altitude of 350 m. They estimated numbers of ducks killed on the marsh (for each species) by multiplying the number of hunters by the average kill for each species found in the bag tally during these years. We used these hunter-effort and kill figures in all calculations for 1975–77.

Field results

Duck numbers on the Delta Marsh varied considerably during the falls of 1973–77 (Fig. 2). The largest estimate recorded was of nearly 100 000, on 17 September 1973, largely due to an abundance of Canvasbacks. The numbers fell during the hunting season, in all years.

Hunter-hours during 1973 and 1974 and hunter numbers during 1975, 1976, and 1977 followed the population trends. Hunter effort was greatest early in all hunting seasons, declining as ducks migrated south (Fig. 3).

Because populations and hunter effort were high early in the season and declined rapidly as the season advanced, our observations included a wide range of waterfowl-abundance and hunter-effort levels. The close correlation between these variables made it difficult to distinguish the effects of migration behaviour, foraging patterns, and weather.

1. Vulnerability

During the 2 years of our decoy trials, 6904 ducks of 11 species responded to our decoys. Our findings deal mainly with Mallard, Canvasback, and Lesser Scaup, the most common ducks on the Delta Marsh during our study.

Canvasback and Lesser Scaup showed less wariness of hunters and their decoys than Mallards (Tables 1 and 2).

We regressed vulnerability coefficients for Mallard, Canvasback, and Lesser Scaup against effort (log base$_{10}$ hours hunted per week) to test the hypothesis (H1) that vulnerability would decrease as cumulative hunting pressure increased. As the correlation was positive, indicating increased vulnerability with increased cumulative effort, we rejected the hypothesis. However, vulnerability was negatively corre-

Figure 2
Duck populations of the Delta Marsh during the falls of 1973–77 as determined by aerial surveys

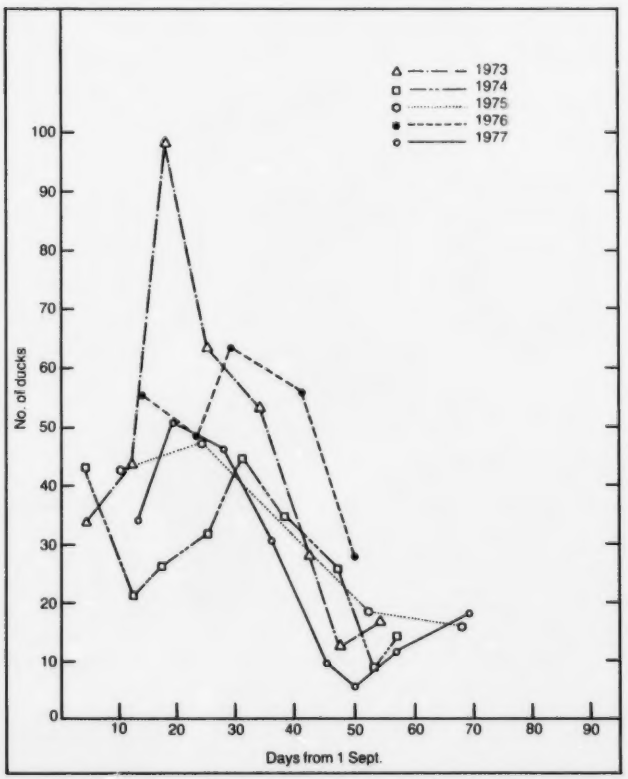
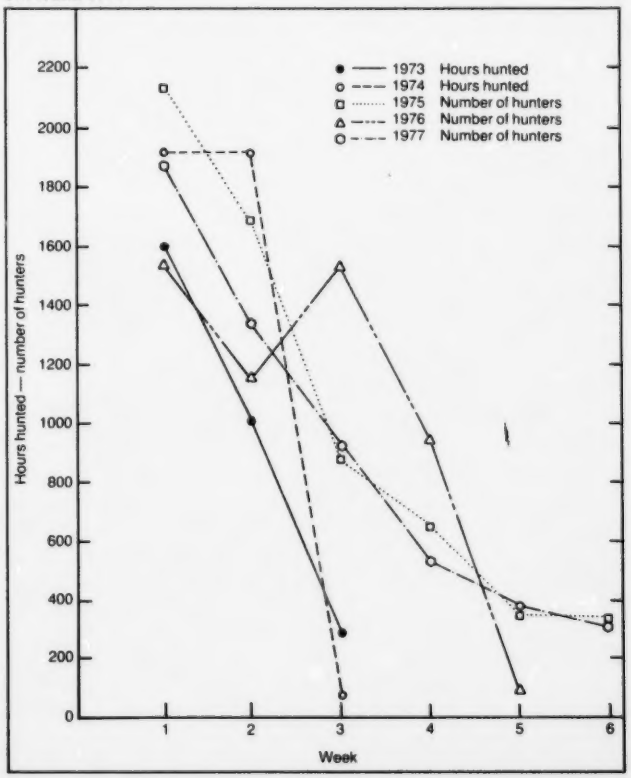


Figure 3
Estimated hunter-hours during each week of hunting during 1973 and 1974 and estimated numbers of hunters during each week of hunting in 1975, 1976, and 1977



lated with current hunting effort for Mallard ($R^2 = 0.60$, df 4, $0.10 > p > 0.05$, $\hat{y} = 0.00264 - 0.0007x$) and Lesser Scaup ($R^2 = 0.74$, df 4, $0.05 > p > 0.02$, $\hat{y} = 0.0142 - 0.0042x$). There was no significant relationship for Canvasback ($R^2 = 0.03$). Vulnerability seems to be inversely proportional to current hunting effort and we conclude that (1) the short-term (daily) wariness of Mallard and Lesser Scaup is increased through encounters with many hunters, and (2) as duck–hunter meetings decline, so does the degree of wariness. If there is avoidance learning, it is either not retained even through one hunting season, or is masked by other behavioural changes that occur through the fall. In either case, avoidance learning does not protect birds against the lower levels of hunting that occur late in the season.

Diving ducks need open water; Mallards and other dabbling ducks adjust to a much broader pattern of acceptable habitat. Delta Mallards loafed on the protected (unhunted) shore of Lake Manitoba and crossed the marsh morning and evening to feed on agricultural fields. Under heavy gun pressure, the ducks usually flew above gun range. Canvasbacks remained on the marsh throughout their stay at Delta; Lesser Scaup frequently flew back and forth between marsh and open lake. None of the diving ducks visited stubble fields.

At Pasquia, Mallards loafed on the marsh between their periods of field feeding; they were highly vulnerable throughout the day. Under steady gun pressure, the Mallards vacated the Pasquia Marsh after the first week of shooting, shifting to isolated lakes, inaccessible to hunters.

In addition to the vulnerability coefficient, we also measured vulnerability by the number of ducks that were lured to within 35 m of our blind as a percentage of all birds responding. At Pasquia Marsh in 1974, 91.6% (329 of 359) of the Mallards responding during decoy trials were vulnerable prior to hunting. During the first week of hunting the percentage of Mallards vulnerable dropped to 67.8 (720 of 1062). No birds remained after the first week.

At Delta in 1973, 63% of Mallards were vulnerable during the week before hunting. This dropped to 32% during opening week and increased to 58% by the third week of hunting (Table 1). In 1974, 88% of Mallards were vulnerable during the week before hunting (Table 2). Within the first week of hunting this dropped to 40%. Vulnerability increased to 65% during the second week and remained at that level through the season.

Some Mallards at Delta may have departed as they did at Pasquia but we were not able to detect this. It may be

Table 1
Results of 36.8 h of decoy trials during the 1973 field season

Sampling period	Species	Population size*	Birds† <35 m	Total birds responding‡	Percent vulnerable§	No. vulnerable per hour‖	Vulnerability coefficient¶ ($\times 10^{-4}$)
1–6 October	Mallard	17 036	32	51	63	3.56	2.1
	Lesser Scaup	3 454	90	111	81	10.00	28.9
	Canvasback	26 189	163	218	75	18.10	6.9
8–13 October	Mallard	4 163	18	57	32	1.22	2.9
	Lesser Scaup	6 017	64	67	96	4.32	7.2
	Canvasback	11 442	56	106	53	3.78	3.3
15–19 October	Mallard	3 630	34	78	44	3.40	9.3
	Lesser Scaup	4 276	82	105	78	8.20	19.1
	Canvasback	410	34	61	56	3.40	82.9
23–26 October	Mallard	6 851	19	33	58	2.44	3.6
	Lesser Scaup	6 993	60	64	94	7.69	11.0
	Canvasback	888	10	10	100	1.28	14.4

*From aerial surveys.
†Birds attracted to ≤35 m in decoy trials.
‡Total birds attracted to decoys during decoy trials.
§Percent of total birds that were ≤35 m in decoy trials.
‖Birds ≤35 m divided by number of hours of observation.
¶Number vulnerable per hour divided by population size.

Table 2
Results of 45.6 h of decoy trials during the 1974 field season

Sampling period	Species	Population size*	Birds† <35 m	Total birds responding‡	Percent vulnerable§	No. vulnerable per hour‖	Vulnerability coefficient¶ ($\times 10^{-4}$)
30 September –4 October	Mallard	32 866	195	221	88	11.18	3.4
	Lesser Scaup	978	50	50	100	3.27	35.2
	Canvasback	10 216	169	200	85	11.05	10.8
7–10 October	Mallard	25 025	102	254	40	9.36	3.7
	Lesser Scaup	7 475	14	14	100	1.28	1.7
	Canvasback	1 679	79	98	81	7.25	43.2
12–17 October	Mallard	20 521	49	75	65	5.38	2.6
	Lesser Scaup	1 877	23	23	100	2.53	13.5
	Canvasback	759	54	54	100	5.93	78.1
19–24 October	Mallard	5 529	91	137	66	8.83	15.9
	Lesser Scaup	533	43	135	32	4.17	78.2
	Canvasback	1 023	47	58	81	4.56	44.5

*From aerial surveys.
†Birds attracted to ≤35 m in decoy trials.
‡Total birds attracted to decoys during decoy trials.
§Percent of total birds that were ≤35 m in decoy trials.
‖Birds ≤35 m divided by number of hours of observation.
¶Number vulnerable per hour divided by population size.

Table 3
Proportion of ducks using refuges on the Delta Marsh during October, as measured by aerial surveys during 1973

Date	No. of birds in refuges	Total ducks observed	Cumulative hunter hours	% birds in refuges
7 Oct.	310	4080	1606	8
13 Oct.	680	4970	2635	14
18 Oct.	260	1185	2931	22
20 Oct.	220	590	2931	37

Table 4
Summary of F ratios generated by regression analysis of vulnerability as related to selected weather variables
(df 32, $F = 4.15$ for $p<0.05$)

Species	Environmental variable			
	Barometric pressure	Relative humidity	Cloud cover	Wind speed
Mallard	0.94	0.93	4.08	5.65
Lesser Scaup	1.95	0.04	1.43	0.30
Canvasback	0.11	0.06	0.73	0.22

that Mallards did not leave Delta because of the presence of unhunted safe areas, which do not occur in the Pasquia area.

In 1973, Canvasback were 75% vulnerable prior to hunting, decreasing to 53% during opening week. During the last week of hunting, the percentage vulnerable rose to 100 (Table 1). In 1974, Canvasback showed an 85% vulnerability during the week before hunting. During the opening week of shooting, this dropped only four points to 81%, then increased to 100% during the second week of hunting (Table 2).

In 1973, the percentage of Lesser Scaups vulnerable was highest during the season (Table 1). In 1974, 100% were vulnerable prior to hunting, 32% were vulnerable by the last week of the season (Table 2).

These findings suggest that Mallards are sensitive to hunters and that avoidance plays a role in their survival when they use heavily shot marshes. The diving ducks, perhaps because they are less adaptable and because their major feeding and resting areas are concentrated on hunted ranges, remain very vulnerable throughout the season.

Avoidance learning is a short-term behaviour and wariness is not retained through the fall at the observed levels of hunting effort. Early avoidance of blinds and hunters may be in response to the noise of shooting, to which birds later habituate. Possibly birds require more feed later in the season (temperatures are lower and energy requirements may be greater) so that the higher vulnerability results from increased pre-migratory foraging.

Vulnerability also correlated negatively with bird abundance; vulnerability was highest when numbers were small. This was an unexpected result. Possible explanations are (1) food requirements may be greater later in autumn, moving birds into hunting areas; (2) presence of proportionally more young with high vulnerability later in the season; or (3) migration into the study area of naive birds from unhunted areas farther north.

The 1973 aerial surveys indicate that all ducks leave hunted areas as the season advances; Mallards and other dabbling ducks do so earlier and in greater numbers. Besides the lakeshore, there are two other refuges on the Delta Marsh. The relative number of ducks on these unshot ranges increased steadily during the hunting season as cumulative hunting pressure increased (Table 3).

Age may also be important to duck safety during the hunting season. During opening week, 9–14 September 1974 at Pasquia, Mallard vulnerability was 25.3×10^{-4}. At Delta for the opening week, 7–12 October 1974, the vulnerability coefficient for Mallards was 3.7×10^{-4}. The opening day bag at Pasquia showed an adult–juvenile ratio of 1:23.8, whereas at Delta the opening week bag was 1:1.7. To make a more appropriate comparison of the data, vulnerability coefficients for the two ranges were adjusted for marsh size by calculating ducks per hectare and dividing this into the rate of encounter per hour for the sampling period. At Pasquia Marsh the adjusted coefficient for Mallard was 46.01. At Delta it was 7.56, indicating that birds at Pasquia were six times as vulnerable as those at Delta during the 1st week of hunting. We attribute these differences to the larger proportion of immature birds in the more northern population. These limited findings support the observations of Bellrose *et al.* (1961) that populations consisting largely of juveniles are more vulnerable than aggregations of adults. Bellrose *et al.* found a progressive decrease in the ratio of juvenile to adult vulnerability in male Mallards, the ratio being 6.5:1 during the opening week of the season at Havana, Illinois and declining to 1.5:1 toward season's end.

Weather had little effect on the vulnerability coefficients of Mallard, Lesser Scaup, and Canvasback. For each species, we tested the dependent variable (vulnerability for individual periods of decoy trials) in multiple regression analysis using barometric pressure, relative humidity, cloud cover, and wind as the independent variables. The one significant correlation was between wind speed and Mallard vulnerability; when winds are high, Mallards are less wary of hunters (Table 4).

2. Hunter selectivity and observed kill

From spy blinds we observed 61 hunting parties during 1973, 1974, and 1977 on the Delta Marsh and accumulated observations on 179 hunter-hours. Hunters showed little selectivity and passed up only 39 opportunities to kill ducks in 267 encounters (Table 5). They rejected Green-winged Teal, Blue-winged Teal, and Bufflehead more often than the large ducks ($\chi^2 = 20.2$, df 1, $p<0.05$). For all 11 species the correlation of selectivity and duck size, as represented by adult male body weight (Bellrose 1976) was 0.765, $p<0.01$. The retrieved kill per hour and total ducks downed per hour varied between weeks during 1973 and 1974 (Table 6). The largest number of birds retrieved per hour was 2.85 and the most ducks downed (kills and cripples) was 4.0. During most weeks the retrieved kill was less than one

Table 5
Hunter selectivity by species as determined by observation on the Delta Marsh during 1973, 1974, and 1977

Species	Mean wt. ad. ♂♂, kg	Total flocks <35 m	Flocks <35 m fired at	Flocks <35 m not fired at	Percent fired at
Green-winged Teal	0.32	23	16	7	69.6
Blue-winged Teal	0.46	38	27	11	71.0
Bufflehead	0.52	18	13	5	72.2
Shoveler	0.68	9	8	1	88.9
Wigeon	0.82	9	8	1	88.9
Lesser Scaup	0.83	30	25	5	83.3
Gadwall	0.97	4	3	1	75.0
Pintail	1.03	8	8	0	100.0
Redhead	1.11	18	16	2	88.9
Mallard	1.24	76	74	2	97.4
Canvasback	1.25	34	30	4	88.2
Total		267	228	39	85.4

Table 6
Observed kill, kill per hunter-hour, estimated effort, and population size for the Delta Marsh in 1973 and 1974

	Week of season					
	1		2		3	
Year	1973	1974	1973	1974	1973	1974
Observed total kill*	2 088	1 382	896	808	195	205
Retrieved kill/hour†	1.30	0.72	0.87	0.42	0.66	2.85
Total ducks downed/hour†	3.10	1.10	1.70	0.85	1.30	4.00
Effort (total hours)‡	1 606	1 919	1 029	1 924	296	72
Population size	27 747	36 605	11 695	25 025	15 574	8 350

*From bag tally.
†From spy blinds.
‡Calculated by observed total bag/(retrieved kill/hour).

Table 7
Hunter success on the Delta Marsh as determined by hunter bag checks during 1973–77

Date	No. of hunters checked	Observed ducks bagged	Ducks/ hunter	Hours/ hunt	Legal daily duck limit
1973	968	1437	1.48	1.63	8
1974	555	765	1.38	1.75	6
1975	994	1755	1.77		6
1976	419	1165	2.78		8
1977	797	969	1.22		6

bird per hunter-hour, suggesting that few hunters fill their bags during a single hunt. The overall bag per hunter-hour was 0.91 in 1973 and 0.79 in 1974. Dividing these values into the mean daily bag per hunter for 1973 and 1974 gives estimates of the mean time per hunt, 1.63 h in 1973 and 1.75 h in 1974 (Table 7).

These spy blind observations are supported by the Delta Marsh bag check (Table 7). In the 5 years of the study, average hunter bags were less than two ducks except in 1976, when the average daily bag was 2.78. The average number of ducks was considerably less than the daily bag limit (Table 7).

3. Handling time

We compared the mean time between an unsuccessful encounter (birds fired upon) and the next encounter with the mean time between a successful encounter and the next encounters and used the difference as a measure of handling time. At any time between an unsuccessful and a subsequent encounter hunters are presumably ready to fire on birds. The time between an encounter when a bird is killed and the next encounter when the hunter is ready to fire includes a period when the hunter is not able to react. We assumed that the difference between these two encounter rates would represent time when a hunter was reloading the gun, pursuing cripples, or retrieving downed birds.

We observed 3796 min of handling time. The mean time between an unsuccessful encounter and the next encounter was 9.31 min (S^2 = 23.79) whereas the mean time between an encounter where birds were killed and the next encounter was 9.29 min (S^2 = 17.42). These findings suggest no significant handling time effect, as the two refractory periods are the same with no measurable period where a hunter is non-reactive. This suggests that hunters do not pursue cripples, retrieve birds, or otherwise relax their vigilance when there is a possibility of killing another bird. Non-linear kill patterns do not result from handling-time constraints.

4. Relation of flock size to probability of mortality

The probability of ducks being wounded or killed (the ratio of birds downed to birds fired upon) when passing a hunter nearer than 35 m was 0.21 whereas at farther than 35 m the probability of being killed was 0.11 (Table 8). These figures are not adjusted for flock size and do not take into account the number of hunters present. The results change considerably when the probability of being killed is related to flock size (Fig. 4*a*). Here the chance of a duck being killed in a flock is calculated by the ratio of birds killed to birds fired at in each flock category. The data indicated that probability of mortality decreased with increasing flock size. However, a hunter is not less likely to hit any bird that he shoots at when that bird is in a large flock. We have adjusted these data by calculating mortality per hunter (Fig. 4*b*). We divided the average number of shots fired per hunter, at flocks of a given size, into the number of shots required to down a bird from a flock of that size to determine the number of encounters required to down one bird, which we then multipled by the flock size (see footnotes to Table 9). The mortality rate is then the reciprocal of the number of birds required by one hunter to kill a single duck.

Flock size is a component of vulnerability because the probability of mortality for the individual declines as the number of its companions becomes larger. Small flocks of 5 or less approached the decoys most frequently in our trials. For Lesser Scaup, 76% in 1973 and 94% in 1974 of small flock encounters were less than 35 m. Of the small flocks of Canvasback, 79% in 1973 and 87% in 1974, and of the small flocks of Mallard, 65% in 1973 and 73% in 1974 came to within less than 35 m of our blinds.

From spy blinds we found the average flock size to be less than three for all species except Lesser Scaup (4.79 in 1974, Table 10). By regressing probability of mortality against flock sizes one through five, probabilities of mortality for the average flock sizes of each species were determined (Table 10). The linear relationship between mortality and flock size for birds less than 35 m from hunters' blinds was significant (R^2 = 0.83, df 3, $p<0.05$, $\hat{y} = 0.25 - 0.0355x$). Species-specific probabilities of mortality for mean flock sizes were calculated using the linear equation (Table 10).

The size of flocks of flying Mallards increased as the season advanced. We regressed mean flock size per week against cumulative hunting effort for Mallard to see if these changes could explain the relationship between vulnerability and hunter effort. The prediction tested was that mean flock sizes would increase due to the advantages for individuals of larger flocks. We did not find a correlation (R^2 = 0.27, $p>0.05$, df 4); this suggests that the increasing flock size may not be a response to hunting effort and is not sufficient to explain the observed effort–vulnerability relationship.

Table 8
Probability of being killed or wounded in relation to range from hunters' blinds on the Delta Marsh (1973, 1974)

	Total birds shot at <35 m	Birds downed <35 m	Probability of mortality	Total birds shot at >35 m	Birds downed >35 m	Probability of mortality
1973	525	92	0.17	328	48	0.15
1974	166	56	0.34	309	25	0.08
Total	691	148	0.21	637	73	0.11

Figure 4
(*a*) Probability of death in relation to flock size as determined from spy blinds on the Delta Marsh during 1973 and 1974 and (*b*) relationship between probability of death and flock size as determined from spy blinds on the Delta Marsh during 1973 and 1974, adjusted for one hunter

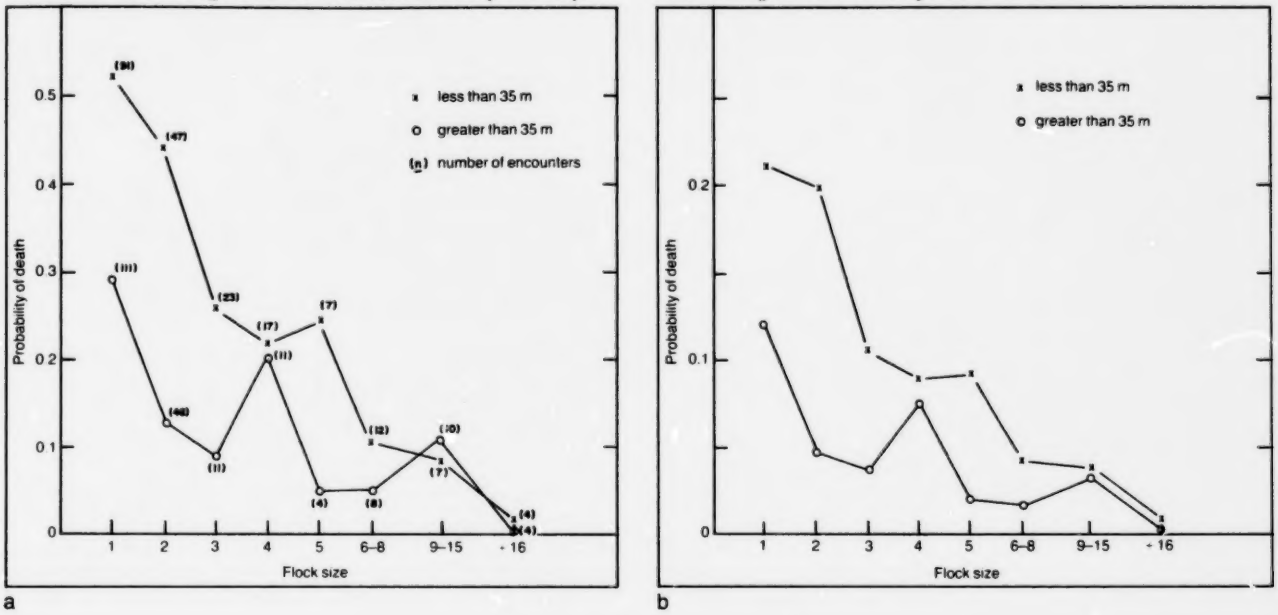


Table 9
Calculations* of probability of one hunter killing a bird showing adjustment for flock sizes and hunters

Flock size	No. of flocks	No. of birds downed	Potential no. of birds available	% of potential downed	No. shots fired	Av. no. hunters present per encounter	Av. no. of shots fired per encounter per hunter (1)	Shots per downed bird (2)	Av. no. of shots per encounter	No. of encounters to down one bird (3)	No. of birds to down one bird (4)	Probability of one hunter killing a bird, % (5)
1	91	47	91	52.7	213	2.5	0.94	4.4	2.3	4.7	4.7	21.3
2	47	38	94	40.4	117	2.0	1.23	3.1	2.5	2.5	5.0	20.0
3	23	18	69	26.1	51	2.5	0.89	2.8	2.2	3.1	9.3	10.8
4	17	15	68	22.1	51	2.3	1.21	3.4	3.0	2.8	11.2	8.9
5	7	9	35	25.7	48	2.9	2.40	5.3	6.9	2.2	11.0	9.1

*Example using flock size 2. If 1.23 shots were fired per encounter (1) and 3.1 (2) shots were required to down a bird 3.1/1.23 = 2.5 (3) the number of encounters required to kill one duck. Flock size multiplied by number of encounters yields number of birds (4). Probability of one hunter killing a bird is the reciprocal of (4) = (5).

Table 10
Mean flock sizes of ducks lured to decoys and probability of mortality based on flock size

Species	1973 $\bar{x}$	1973 *n*	1973 SE	1973 Probability of mortality <35 m	1974 $\bar{x}$	1974 *n*	1974 SE	1974 Probability of mortality <35 m
Blue-winged Teal	1.48	35	0.18	0.19	1.00	7	trace	0.21
Bufflehead	2.20	41	0.24	0.16	1.89	38	0.17	0.18
Canvasback	2.83	366	0.16	0.15	2.76	209	0.22	0.15
Gadwall	1.90	71	0.19	0.17	1.95	86	0.15	0.18
Green-winged Teal	1.90	30	0.40	0.17	1.37	38	0.11	0.20
Lesser Scaup	2.90	209	0.20	0.14	4.79	62	1.47	0.08
Mallard	2.53	389	0.17	0.16	2.71	313	0.25	0.15
Pintail	1.58	109	0.14	0.19	1.75	48	0.19	0.18
Redhead	2.00	57	0.24	0.18	1.58	82	0.14	0.19
Shoveler	1.64	28	0.33	0.19	1.21	71	0.06	0.20
Wigeon	1.79	53	0.15	0.18	1.40	35	0.13	0.20

5. Density–kill relationship

In a simple predator–prey system, quarry should be encountered in proportion to their abundance (Holling 1957*b*). Therefore, we regressed encounter rates from decoy trials against population to determine whether the kill patterns for the three species were related to population and whether the rate of encounter could be treated as random. There was a positive trend for Mallard ($R^2 = 0.34$, df 4, $p>0.05$) but not for Canvasback or Lesser Scaup. These findings suggest that kill should be a non-linear function of density even if the effects of handling time are ignored.

Our shooting at passing birds to avoid habituation to our decoy trial blinds may have introduced a bias in this analysis: the decoy trial observations may include an artificial handling time associated with each flock that was shot at. This would result in a saturating (non-linear) encounter pattern, as modelled by the Holling (1959*a*) disc equation.

We further analysed our spy blind data to see if time between encounters was independent of population size. We calculated mean time between encounters where shots were fired for periods where population estimates were available during 1973, 1974, and 1977. We then regressed time between encounters with population size and found only a slight negative correlation with a slope near zero ($\hat{y} = 10.867 - 0.00007x$, $R^2 = 0.12$, $p>0.05$). We found that time between encounters is independent of population size and that there is a relatively constant refractory period after a gunshot. The time between encounters is constrained by bird behaviour and there is a refractory period that must elapse after gunfire, before ducks again approach the area where the shots were fired. This approximately 9-min period would result in hunters' bags showing a non-linear kill pattern. This is the more likely as ducks are active only for short periods during certain times of the day.

6. Analysis of hunter bag data

To further investigate the relationships between kill and population and hunter effort, we performed a multivariate analysis of the 1975, 1976, and 1977 census and bag data. Table 11 shows estimates of population size, kill, and hunter numbers. We adjusted hunter numbers according to hours of effective search per hunt. In the analysis we

Table 11
Estimated kill, population size, and hunter numbers at Delta for selected weeks during 1975, 1976, and 1977

	Mallard		Lesser Scaup		Canvasback		Est. no.
Week	Est. kill*	Pop. size†	Est. kill*	Pop. size†	Est. kill*	Pop. size†	of hunters
1975							
6–11 Oct.	1151		819		376		2145
13–18 Oct.	447		668		507		1691
20–25 Oct.	365	4 848	259	7 408	191	2 584	879
27 Oct. – 1 Nov.	493		445		158		647
3–8 Nov.	163	4 656	144	8 312	15	768	340
10–15 Nov.	180		94		9		326
1976							
27 Sept. – 2 Oct.	1265	9 185	1244	4 286	454	19 069	1543
4–9 Oct.	333		454		126		1149
11–16 Oct.	506	7 807	1395	21 235	236	18 400	1530
18–23 Oct.	655	8 634	1144	12 864	171	2 235	944
25–30 Oct.	100		3		2		89
1977							
3–8 Oct.	733	15 484	666	7 939	216	3 167	1879
10–15 Oct.	518	4 064	671	5 064	148	18‡	1342
17–22 Oct.	553	3 754	524	1 426	58	115	919
24–29 Oct.	327	2 592	499	8 084	20	40	536
31 Oct. – 5 Nov.	506		370		12		372
7–12 Nov.	94	14 648	7	3 208			310

*Estimated kill.
†Population estimate.
‡Data set not included in analysis.

Table 12
Crippling losses in relation to range from hunters' blinds on the Delta Marsh (1973, 1974, 1977)

	<35 m			>35 m			Total		
Year	No. killed	No. crippled	% crippled of downed birds	No. killed	No. crippled	% crippled of downed birds	No. killed	No. crippled	% crippled of downed birds
1973	65	27	29.3	21	27	56.3	86	54	38.6
1974	41	15	26.8	13	12	48.0	54	27	33.3
1977							23	9	28.1
1973,1974 Total	106	42	28.4	34	39	53.4	140	81	36.7
1973,1974, 1977 Total							163	90	35.6

assumed that hunters spent 2 h actively hunting ducks on each occasion. In 1973 and 1974 we found the average hunt to be about that length. A simple model that represents basic constraints and possible non-linearities in the harvesting process would be

$$k = \mathrm{x}\, N^{\alpha} E^{\beta}$$

where k = kill, N = population size, E = effort, and x, α and β are fitted constants. Non-linearity of the kill per hunter functional relationship will be indicated by $\alpha \neq 1.0$. Converting the equation to logarithms gives the multivariate linear form:

$$\hat{Z} = \log \mathrm{k} = \mathrm{x} + \alpha \log N + \beta \log E$$

For Mallard the equation is highly significant ($R^2 = 0.83$, df 7, $p<0.05$), suggesting a significant relationship between kill, Mallard numbers, and hunter effort. The equation resulting from the Mallard analysis was $\hat{Z} = -0.575 - 0.19\,(\log N) + 1.1\,(\log E)$. For Lesser Scaup the relationship was significant [$R^2 = 0.67$, df 7, $p<0.05$, $\hat{Z} = -11.9 + 0.46\,(\log N) + 1.8\,(\log E)$]. Canvasback kill was also correlated with effort and numbers [$R^2 = 0.87$, df 5, $p<0.05$, $\hat{Z} = 8.5 + 0.19\,(\log N) + 1.6\,(\log E)$]. Thus, a logarithmic model relating kill to population size and hunter effort describes kill patterns of the three species. Furthermore, the α values were all < 1.0, consistent with a non-linear, saturating functional response per hunter in agreement with the experimental decoy trial and bag-check results. The β values were all > 1.0, suggesting that hunters facilitate one another's chances of finding birds.

7. Allocation of hunter effort

Duck populations and hunter effort declined as the hunting season progressed during all years. During 1973 and 1974 there was a positive linear correlation between hours hunted per week and duck population size for each week ($R^2 = 0.74$, df 4, $\hat{y} = 208.3 + 0.065x$, $p < 0.05$). During the 1975, 1976, and 1977 seasons the relationship between numbers of hunters and of ducks was also significant ($R^2 = 0.70$, df 9, $p < 0.05$, $\hat{y} = 374.9 + 0.025x$).

Throughout the 1973–77 study, estimated hunter effort decreased as the hunting season progressed. This may be related to the onset of cold weather or it may mean simply that hunters lose interest.

8. Crippling losses

The study of hunter behaviour is complicated by unretrieved crippled birds. We found crippling losses to be similar during the first 2 years of our study, 38.6% in 1973, 33.3% in 1974, with a mean of 36.7%. The percentage crippled was significantly higher, 53.4, for birds fired upon when more than 35 m from a hunter; compared with 28.4% for birds shot at within 35 m ($X^2 = 13.21$, df 1, $p < 0.05$). The crippling loss was little altered to 35.6%, by the inclusion of 1977 data (Table 12).

Discussion

Holling (1959*b*) pointed out that subsidiary components of predation such as prey characteristics affect the basic functional response of predators to prey density. Holling (1966) also suggested that avoidance learning by prey was one explanation of why fewer prey may be consumed as prey density rises.

By learning to avoid certain situations ducks improve their survival rate in the presence of hunters. Melzack (1961), working with Mallard ducklings, found that birds readily habituate to model predators. Hochbaum *et al.* (1954) found that field-feeding ducks learned to avoid scarecrows that were frequently moved about. The effectiveness of these scarecrows was in some cases reinforced by gunfire; however, no ducks were killed. Thorpe (1963) suggests that prey responses to predators are not instinctive, rather prey tend to avoid novel, high intensity, or sudden stimuli.

There are several explanations of how such learning may occur. Experience depends on age and the degree of exposure to hunting. We expected vulnerability to decrease with cumulative experiences with gunners and we assumed at the outset that avoidance learning would be reinforced by gunfire. This holds for white-tailed deer (*Odocoileus virginianus*) which become less vulnerable as the cumulative hunting pressure increases (Roseberry and Klimstra 1974). However, we found that duck vulnerability is related to current hunting effort. The most intensive hunting at Delta occurs early in the season; ducks are most wary immediately after opening day. As the hunting season progresses, vulnerability increases.

On a fine scale Mallards and Lesser Scaups learn to recognize hunters as dangerous by direct experience with occupied blinds. Individuals and flocks soon associated certain parts of the marsh with the loud, startling activity of hunters. Shortly after the hunting season opened, these two species avoided loafing and feeding near shooting stands and they were least vulnerable during the first week. On a broader scale some ducks learned to avoid hunted areas at Pasquia and Delta by relocating to refuges and sites inaccessible to hunters. A biotelemetry study of marked birds in Minnesota revealed that waterfowl form mixed species flocks that avoid hunting areas and restrict their activities under heavy gun pressure (Kirby *et al.* 1976).

Our belief that vulnerability is related to hunter effort is supported by Bellrose's (1944) findings in Illinois where the total daily bag increased to a point at which more hunters resulted in lowered or stationary daily bags. He attributed this to marshes having a limited carrying capacity for hunters, beyond which there is so much interference and out-of-range shooting that the kill may even decline. Bellrose also found that the fewer the hunters, the greater was the indi-

Table 13
Possible influences of independent variables on the kill of ducks as predicted by three models

	Model type		
Variables	Linear model	Holling type 2 predator–prey model	Total kill logarithmic model
Encounter or kill rate	Slope constant over time	Encounter rate not constant	antilog regression X
Population size	Kill proportional to duck abundance	Other species present influence handling time	$\alpha<1$ implies (1) bird clumping (2) handling time effect
Hunter effort	Kill proportional to hunter numbers	Vulnerability dependent on effort	$\beta>1$ implies hunters help one another $\beta<1$ implies mutual interference among hunters

vidual success. Bergerud *et al.* (1968) found in Newfoundland that the success of Moose (*Alces alces*) hunters was inversely related to hunter density.

The analysis of vulnerability may be summarized three ways: the linear model, the type 2 predator–prey model, and the total kill logarithmic model (Table 13). The first model assumes a random encounter process which was not the case at Delta. The second model (Holling 1959*a*, 1959*b*) assumes that prey characteristics that reduce chances of capture (e.g. avoidance learning on the part of ducks) and that predator characteristics such as "handling time" place constraints on total kill. Our data relating vulnerability to hunter effort support this model.

Further appraisal may be accomplished using the regression coefficients of the third model. For Mallard α was significantly less than 1.0 ($t = 5.9$, df 7, $p<0.05$), indicating a non-linear relationship between kill and population size. This is consistent with the observation that hunters search non-randomly and birds are distributed contagiously. Alternatively, there is a significant handling-time effect, the time lost per encounter being great enough to limit the bag. This would be especially likely if ducks fly only for short periods each day. The regression coefficient β was not significantly different from 1.0 ($t = 0.54$, df 7, $p>0.05$), suggesting no interference among hunters. This suggests that our finding relating vulnerability to hunter effort may be misleading and that increased vulnerability through the season is due to some intrinsic change in bird behaviour or else some effect associated with decreasing population size.

For Lesser Scaup α was less than 1.0 but not significantly so ($t = 1.18$, df 7, $p>0.05$). The regression coefficient β for Lesser Scaup was greater than 1.0 although not significantly so ($t = 1.572$, df 7, $p>0.05$).

For Canvasback the regression coefficient α was significantly less than 1.0 ($t = 6.4$, df 5, $p<0.05$), suggesting a handling time effect or non-random search associated with clumped distribution of ducks. The coefficient β was not different from 1.0 ($t = 1.3$, df 5, $p>0.05$) suggesting no hunter interference.

Overall, the regression coefficients indicate that vulnerability may be the result of intrinsic behaviour, such as flocking due to increased pre-migratory food requirements. This analysis indicates that hunters did not interfere with each other. For Lesser Scaup, hunters may help one another by scaring birds from one area to another. Thus, we conclude that avoidance learning, as observed at Delta, is a short-term behaviour of ducks frightened by heavy gunfire early in the season.

The statistical model of the bag-check data supports the hypothesis that contagious bird distribution and non-random search patterns by hunters result in a saturating relationship between kill and population size. Our analysis of the spy blind data sugests that mean time between encounters is independent of duck density, due to a behavioural refractory period after each shot fired. Handling time does not constrain hunters and has no influence on bag size.

We found that different species approached the zone of greatest danger to ducks (within 35 m of hunters' guns) in different ways. Mallard, the most wary ducks at Delta, are abundant throughout North America. Canvasback, less wary and more easily killed, have declined in recent years. We suspect that specific differences in response to hunters may be one important reason for the relative success of the Mallard. Stott and Olson (1972) attribute differences in numbers of three species of sea ducks along the New England coastline to variations in vulnerability to hunters.

Although most hunters believe that ducks are readily attracted to decoys during windy, wet, cloudy days, we found little correlation between quantitative measures of weather and vulnerability. The only significant relationship was between wind speed and the opportunity to kill Mallards. Our findings suggest that fall weather has little influence on vulnerability of the three species. On the other hand, Koerner *et al.* (1974) found the kill of Canada Geese (*Branta canadensis*) was significantly correlated with barometric pressure and temperature.

Differences in the flight characteristics of species may influence hunter selectivity. For instance, hunters were less likely to shoot at Green-winged Teal, Blue-winged Teal, and Bufflehead than the larger ducks. Boyd (1971) reported similar findings for small ducks in eastern Canada. There is an element of surprise favouring smaller ducks. They catch a hunter's eye less quickly and their manoeuvrability allows the smaller birds to swing suddenly to the decoys. Hunters infrequently fired upon ducks making abrupt approaches or coming from behind.

The density and quality of alternate food or "buffer species" (Leopold 1933) and the willingness of the predator to exploit other prey are important variables that affect the kill. The functional response of the principal prey may be slower when the kinds and palatability of "buffers" increases (Holling 1966). In that case, hunter selectivity has an important effect on size and species composition of the duck kill. We found that hunters took large rather than small ducks but we do not know whether this was deliberate or due to physiological (size, flight speed, and manoeuvrability) and behavioural differences among species. We have no evidence that small ducks serve as "buffer" species.

We found that hunters shot indiscriminately even when regulations were in place to protect species such as Canvasback. Geis and Crissey's (1973) study of the "point system" in the US showed this, too. There, in states that choose to use this system, the legal daily bag depends on numerical values allotted to each species (in some, differently to males and females) according to its rarity. The killing of one Canvasback or Redhead, for example, limits the hunter to not more than one additional duck in her or his daily bag. The day's hunt must end if he or she has killed other birds. Geis and Crissey found that hunters fired on over 90% of flights of Canvasback and Redhead.

This lack of hunter selectivity has implications for management. Many states and provinces attempt to protect

certain species by limiting the number of specimens allowed in the daily bag. However, hunters do not refrain from shooting ducks that are protected by game laws (this study, Hochbaum and Caldwell 1977). Most hunters seem unable to identify waterfowl in flight adequately (Evard 1970).

Our findings linking the probability of being killed to flock size support those of Olson (1965) and Boyd (1971), who demonstrated that the probability of a duck being shot decreases with increasing flock size. Powell (1974) suggested that membership in a large flock was an effective anti-predator strategy. Powell's (1974) work with Starlings (*Sturnus vulgaris*) demonstrates that large flocks detect predators more quickly than do single birds. Siegfried and Underhill (1975) drew a similar conclusion for Laughing Doves (*Streptopelia senegalensis*). We noticed that when one duck in a flock flared, the entire flock would flare, although all may not have noticed our presence. This social facilitation has high survival value. When they flare, the birds turn quickly and fly away from danger, thus presenting a more difficult target.

The overall crippling loss of 35.6% in our study is higher than losses reported from field studies in eastern Canada, in which Boyd (1971) observed a crippling loss of 24.8%. This is similar to the 22.5% cripples found in Bellrose's (1953) survey and higher than the 16% found by Geis and Crissey (1973), both in the US. Sowls (1955) questioned experienced hunters on the Delta Marsh in the late 1940s and found 36% crippled (394 birds lost) in a bag of 705 ducks, which agrees with the 35.6% crippling loss in our study.

In summary, we found that vulnerability is not related to cumulative hunting effort, rather it is a function of current hunting effort. The results were not definitive, however, because vulnerability increased as the season progressed and populations fell. Further research is required to evaluate the effects of pre-migratory foraging requirements, age, and migration patterns on vulnerability. This would require visible or radio-marking of individual birds.

We found differences in vulnerability by species as was predicted. Kill was not a linear function of duck abundance; so hunters must search non-randomly. Handling time per bird shot or crippled is not high enough to limit the daily bag and time between encounters is independent of population size, resulting in a saturating kill pattern. We demonstrated that hunter effort correlates with bird abundance but this may only be related to tradition, cold weather, or loss of interest. Hunter interviews might reveal more about how hunters allocate effort. Contrary to most hunters' belief, vulnerability is not related to local weather conditions. Although current species management policy assumes that hunters can discriminate between species, hunters were not selective, even when required to be by law.

Our limited resources, unmarked birds and, in some instances, small sample sizes, led to some weaknesses in the study. In several calculations we pooled species. Also, we had to assume that technical aspects of surveys were constant.

Several untested assumptions were inherent in the study. For example, in calculating the vulnerability coefficient for any week, we assumed that the population size was uniform throughout the week. In addition, the distance of ducks from our experimental blinds could only be estimated as less than, or greater than, 35 m. We assume the error associated with distances is constant because estimates were made by the same observer during both years. We also assume the coefficient is independent of population size and reflects only behavioural differences during the study period. The risk to a bird passing a hunter is also treated as homogeneous throughout the time for which the coefficient was calculated. The calculations do not include the effects of habituation and age ratios. We assumed birds did not habituate to our blinds because we provided negative reinforcement during experimental hunts. Neither habituation nor age-ratio factors could be incorporated into the vulnerability coefficient because the population was not marked.

In the calculation of hunter effort we assume constant effort per bird shot during each survey week and also assume that sample sizes are large enough to provide the same general level of hunting skill in each. The calculation of hunter effort assumes that hunters' techniques are uniform from year to year. The calculated values reflect an index of hunter effort.

When we calculated crippling losses and probability of mortality, we had to pool species because samples were small. Therefore, we assume that crippling losses and probability of being killed are the same for all species.

Several problems were associated with estimating waterfowl abundance from the air. Replication of counts was not possible so there is no estimate of sampling precision. We assume that all birds present along the transects were actually seen, and believe that the survey is a representative index of species present. We assigned a species to unidentified ducks by assuming the proportions would be the same as among the population of known species. In addition, the aerial survey gave no indication of the rate of replacement of dead or departed birds by newcomers.

Mathematical model for a single hunter

1. Background to the model

Birds and hunters interact in a complex fashion through each hunting season. Simulation modelling is one means to capture some of this complexity, in order to address such questions as: If vulnerability decreases with increasing effort, is it necessary to regulate hunter effort at all and, if so, how can particular target harvests be achieved? What are the implications for the kill of one species of changes in the abundance of other species, given that hunting effort may increase with increased combined bird densities whereas increased availability of other species may tend to decrease the pressure on the species under consideration? Our field results will be useless or even misleading to managers unless the data can be tied together in an overall predictive framework.

A multi-species model is necessary for several reasons. From the standpoint of the manager, it would be ideal to regulate hunting of each species independently, because more birds could be killed than if all are subject to the same regulations (Ricker 1958). In addition, Ricker pointed out that if several species are harvested at one rate, one species may become relatively more abundant whereas others may decline. However, several characteristics of ducks and hunters make yield management for individual species unattainable. First, duck populations in the fall consist of many species, and hunters shoot indiscriminately. Ducks also have species-specific vulnerabilities and behaviour patterns. If managers design regulations to achieve a high kill of Mallard in a certain area and Canvasback are also present, the Canvasback kill will be large because of their greater vulnerability.

Holling (1959*b*) developed a single-species model of the functional response of a predator to prey density which predicts that as prey density increases, the number of prey taken per unit time will rise at a decelerating rate to a threshold level (Type 2 predation) (Fig. 5). In the next section we examine Holling's model in relation to multi-species waterfowl harvests using our data from the Delta Marsh. Holling's equation was well suited to our data because it could be used to show the rate of kill per hunter as a function of bird abundance. The features that Royoma (1970) added to the model — (1) the allocation of hunting effort between areas and periods of differing prey density and (2) mutual interference of predators as a function of prey density — are necessary because we postulate that hunting effort correlates with bird density, and that decreasing vulnerability of ducks when hunter effort is high may be evidence of mutual interference by hunters.

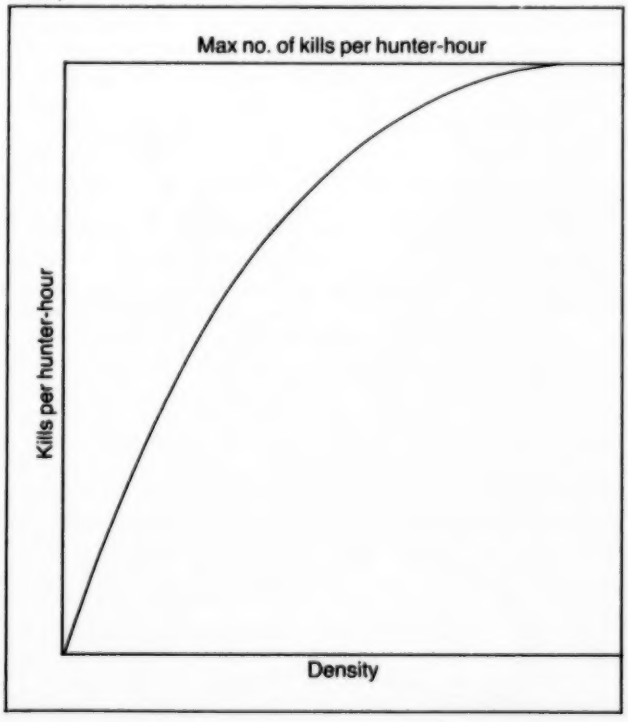
2. Quantifying the model

The model assumes that, in the absence of regulations, the bag per hunter-hour will increase with duck density until the kill reaches a limit due to handling time (Fig. 5). The kill rate per hunter as a function of duck density is derived from Holling's (1959*a*) disc equation:

$$N_c = \frac{aN_0}{(1 + bN_0)} \qquad [1]$$

where: N_c = prey caught,
N_0 = prey density,
a = encounter rate of predator with prey, times total time per hunt, times probability of kill per encounter,
b = handling time per prey encountered, times a

Figure 5
Functional relationship between potential kill per hunter-hour and duck density



This equation is for a predator that consumes one prey type. For n prey species, the multi-species analogue for equation [1] is (Charnov 1973):

$$N_r = \frac{T_s \sum_{i=1}^{n} \lambda_i}{T_s + T_h} \qquad [2]$$

where: λ_i = encounter rate of i^{th} prey species.
T_s = total time spent searching for prey.
T_h = total time spent handling prey.

and $T_h = \Sigma \lambda_i T_s h_i$

where: h_i = handling time for each prey individual of the i^{th} species.

$$\text{so that: } N_r = \frac{T_s \sum_{i=1}^{n} \lambda_i}{T_s + \sum_{i=1}^{n} \lambda_i T_s h_i} = \frac{\sum_{i=1}^{n} \lambda_i}{1 + \sum_{i=1}^{n} \lambda_i h_i} \qquad [3]$$

as: $\lambda_i = a_i N_i$,

where: a_i = the vulnerability coefficient for the i^{th} species, times probability of mortality per encounter for species i, times selectivity for species i,

and N_i = density of i^{th} species,

$$\text{so that: } N_r = \frac{\sum_{i=1}^{n} a_i N_i}{1 + \sum_{i=1}^{n} a_i N_i h_i} \qquad [4]$$

If h_i is the handling time for one individual of prey species i then $1/h_i$ will be the maximum rate of killing of species i. Let $1/h_i = m$, the maximum potential kill. Then,

$$N_r = \frac{\sum_{i=1}^{n} a_i N_i}{1 + \sum_{i=1}^{n} a_i N_i / m} \qquad [5]$$

Now assume that m_i and h_i are the same for all species of ducks, then

$$N_r = \frac{\sum_{i=1}^{n} a_i N_i}{1 + (\sum_{i=1}^{n} a_i N_i)/m} \qquad [6]$$

and for the i^{th} species

$$N_{ir} = \frac{a_i N_i}{1 + (\sum_{i=1}^{n} a_i N_i)/m} \qquad [7]$$

The a_i values in this equation are the vulnerability coefficients times probability of mortality times hunter selectivity as described in Tables 5 and 10. The vulnerability coefficients (a_i) vary over time in relation to hunter effort so the net response cannot be seen by entering a single set of numbers into the equation. The value of m is taken from hunter observations and is the maximum kill per hunter-hour (4.0 from Table 6). N_{ir} equals the kill rate for the i^{th} species per hunter-hour. This is the multi-species analogue of the disc equation.

Management analysis and implications

1. Applying the model to the Delta Marsh

1.1. Additional assumptions and structure

The multi-species disc equation [7] calculates kill on an hourly basis for one hunter. We incorporated this function into a simulation model that also includes total hunting effort and population-size changes. The simulation then forecasts kill by week for Mallard, Canvasback, and Lesser Scaup. Inputs are the number of weeks, maximum kill rate, initial population sizes, species-specific probabilities of mortality, and hunter selectivity.

We calculate number of hunter-hours as a function of total population size each week employing the equation:

$$E_t = B + 0.065\,D_t \qquad [8]$$

where: E_t = effort at time t,
D_t = total population size at time t,
B = effort level when population size is zero.

We found that effort was correlated with population size. Initial efforts can be varied by changing the B value and thus alternative assumptions about hunter-effort responses can be used to drive the system.

Vulnerability for Mallard and Lesser Scaup is computed dynamically as a function of hunter effort using the linear equations derived from field data:

$$a_1 = 0.00264 - 0.0007\ (\log \text{effort}) \qquad [9]$$
$$a_2 = 0.0142 - 0.0042\ (\log \text{effort}) \qquad [10]$$

where: a_1 = Mallard vulnerability
a_2 = Lesser Scaup vulnerability

Canvasback vulnerability showed no correlation with measured variables and is assumed constant. The value is entered using the mean vulnerability for the 6 weeks of hunting during 1973 and 1974 (44.4×10^{-4}).

We calculate weekly kills for each species by multiplying the estimated week's effort by the hourly kill for each species as predicted by the disc equation [7]. Because no estimates of migrational changeovers are available, we assume a closed system of sub-populations in which the kill is removed and the population updated for the next week by the equation:

$$Ni_{t+1} = Ni_t - Ki_t \qquad [11]$$

where: Ni = population size in week t for species i
Ki_t = kill (including cripples) for species i in week t.

Thus the model dynamically considers effort, population size, and vulnerability and accounts for harvest losses, interference of hunters, and avoidance learning as well as the components of selectivity and species-specific probability of being shot.

A key, and untested, assumption here is that hunters ignore one another; in the model we assume hunters respond to bird density (equation 8) rather than to the number of birds they kill per unit effort.

1.2. Management options

We modified the model to incorporate our field data in order to provide a general evaluation of alternative harvest strategies and to gain insight into the complexities of waterfowl hunting mortality. We did not try to make precise numerical predictions because population levels cannot be forecasted for each week. We created a series of simulations for varying season lengths, effort levels, and bird abundance to appraise the effects on the kill of each species of the following management options: (1) controlling hunter numbers, (2) controlling abundance of ducks; (3) controlling season length.

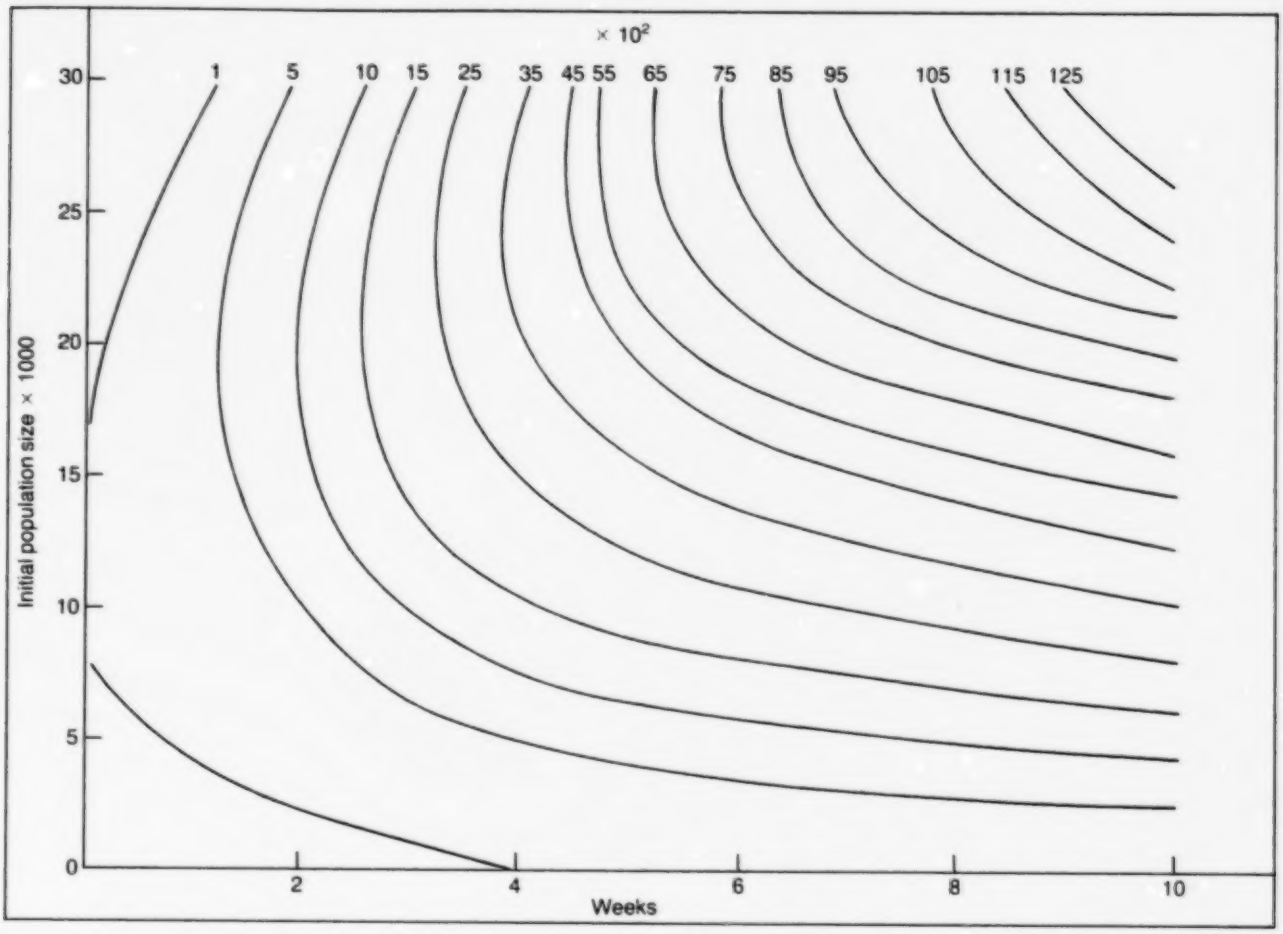
We did not include bag limits, commonly thought to control harvests, in the analysis because few hunters achieve legal daily limits. On a regional scale, bag limits may affect the numbers of hunters who go afield (Christisen 1971); however, we had no data on such responses of hunters to bag limits on the Delta Marsh and therefore could not incorporate this possible response in our model.

2. Results and discussion

The results of simulated management options demonstrate that each species reponds individually to hunter effort and season length (Fig. 6–8). These variations in kill pattern are due to species-specific differences in vulnerability.

Mallard, under various harvest regimes, showed highest kill when the season was longest and the population greatest. Lengthy seasons are needed to obtain intermediate kills at lower population levels; shorter seasons require a large number of birds to achieve similar yields. The analysis revealed that Mallards respond well to hunting pressure: kills are never excessive. For example, with the longest season and highest population, only about one-third of the birds are harvested. When seasons are shortened, the kill of Mallards remains small even when ducks are abundant. The most sensitive situation is when the population exceeds 15 000 and the season is longer than 6 weeks. With a season of 4 weeks or less, the kill is not strongly influenced by population.

Figure 6
Isopleth diagram showing the relationship between regions of Mallard kill and population size and season length under normal effort levels observed at Delta



Kills under low and normal hunting pressure differ only in that the harvest under lower pressure is slightly smaller at similar densities and season lengths. When effort increases above normal, the kill remains unchanged.

In summary, Mallard harvests at Delta are strongly influenced by population size and season length. The ducks have a strong survival response in the face of increased numbers of hunters, and kills remain relatively constant. This is due, in part, to increased wariness. Reductions in hunter effort will produce only a small drop in the overall kill, because the vulnerability of Mallard increases when the number of hunter-hours lessens, thus the kill per hunter-hour also increases. Managers should, therefore, shorten the season to reduce the kill and lengthen it when they want large harvests.

In contrast to the Mallard, which showed largest kills at highest densities, Lesser Scaup suffer small kills when abundant. Greatest kills occur at intermediate densities (Fig. 7), due to the effect of population size on hunter effort and the subsequent depressing effect that hunting pressure has on Lesser Scaup vulnerability. Highest yields are attained in the region of 15 000 birds and a 10-week season with normal hunter-effort levels. Adding weeks to the season does not influence the kill greatly at low or high densities (Fig. 7). Lengthening the season beyond 6 weeks, makes a big difference at intermediate population levels (Fig. 7).

When hunting pressure decreased, the kill of Lesser Scaup became larger than was observed at normal effort levels, due to increased vulnerability; however, when the pressure increased the kill became smaller.

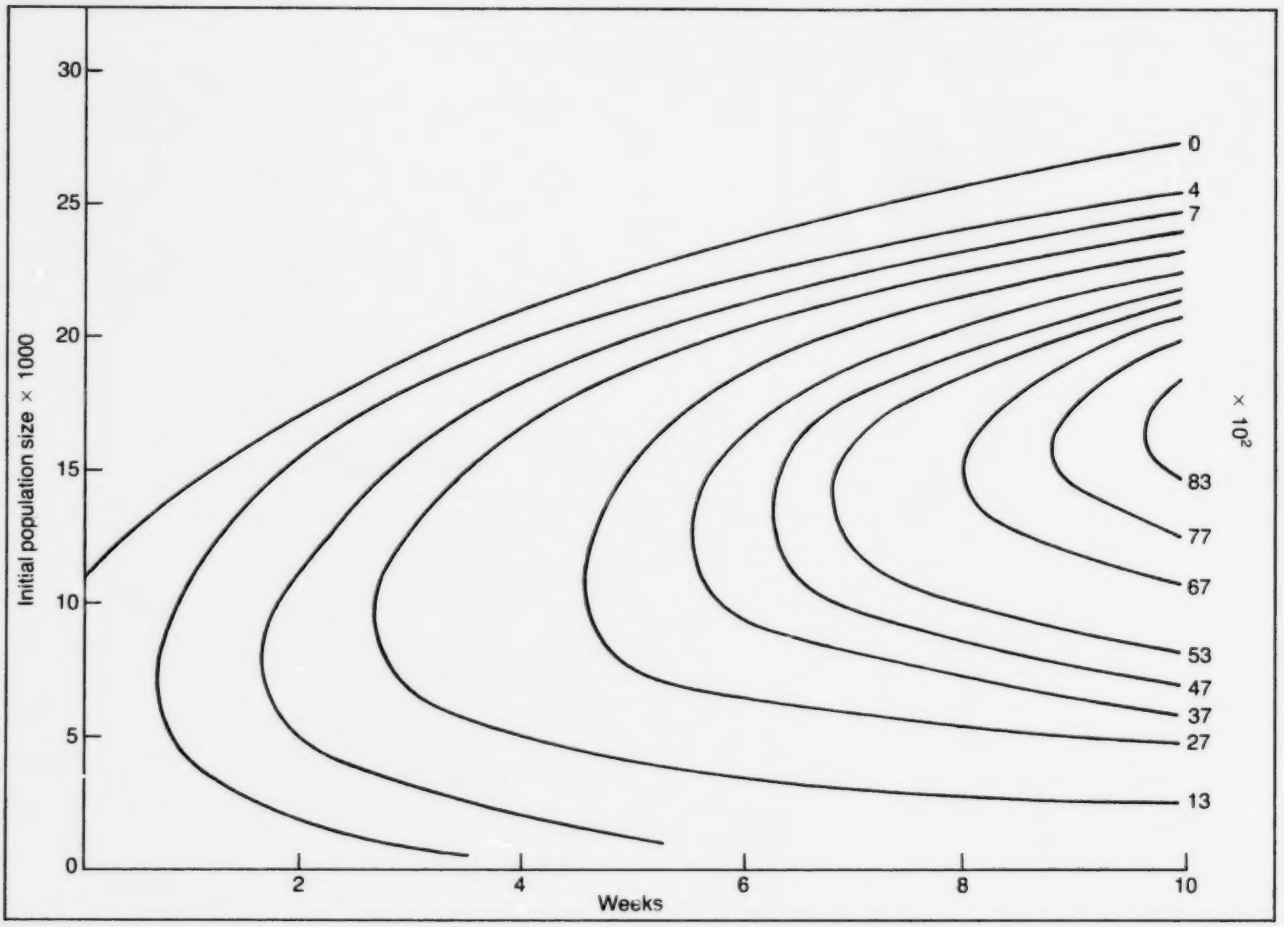
In conclusion, the kill of Lesser Scaup is strongly influenced by both population size and hunter effort. In contrast to the Mallard, the kill does not always increase with population. Season length is not as important as with Mallard, and Lesser Scaup are able to withstand large increases in hunter effort; kills may decline as gun pressure increases. Special regulations are not necessary in the overall management of Lesser Scaup at Delta.

The Canvasback kill is largely dictated by population size (Fig. 8), as was the case with Lesser Scaup. In comparison to Lesser Scaup, however, the kill becomes proportionately larger as the population increases (Fig. 8). The kill of Canvasback is relatively large even if seasons are short. If the population is small, a long season will produce a similar kill to a short season. At high densities, a short season will produce a large kill.

Reducing hunting pressure from the 1973 to the 1977 baseline does not much lower the Canvasback kill. In contrast, increasing the hunter effort will increase the kill, especially at lower Canvasback densities.

Canvasback, unlike Mallard and Lesser Scaup, are not able to respond favourably to changes in gunning pres-

Figure 7
Isopleth diagram showing the relationship between regions of Lesser Scaup kill and population size and season length under normal effort levels observed at Delta



sure. Lengthening the season does not make much difference as large portions of the population are killed even with short seasons. Kill levels of Canvasback are largely a function of population size. The Canvasback requires special protection because of its small continental population; managers should plan seasons of less than 2 weeks when populations are large. However, when the local population is small (5000 range), season length should not be shortened, because the kill will be small irrespective of season length. A shortened season designed to protect Canvasback would unnecessarily deprive hunters of more adaptable species like Mallard and Lesser Scaup.

3. Management implications of findings

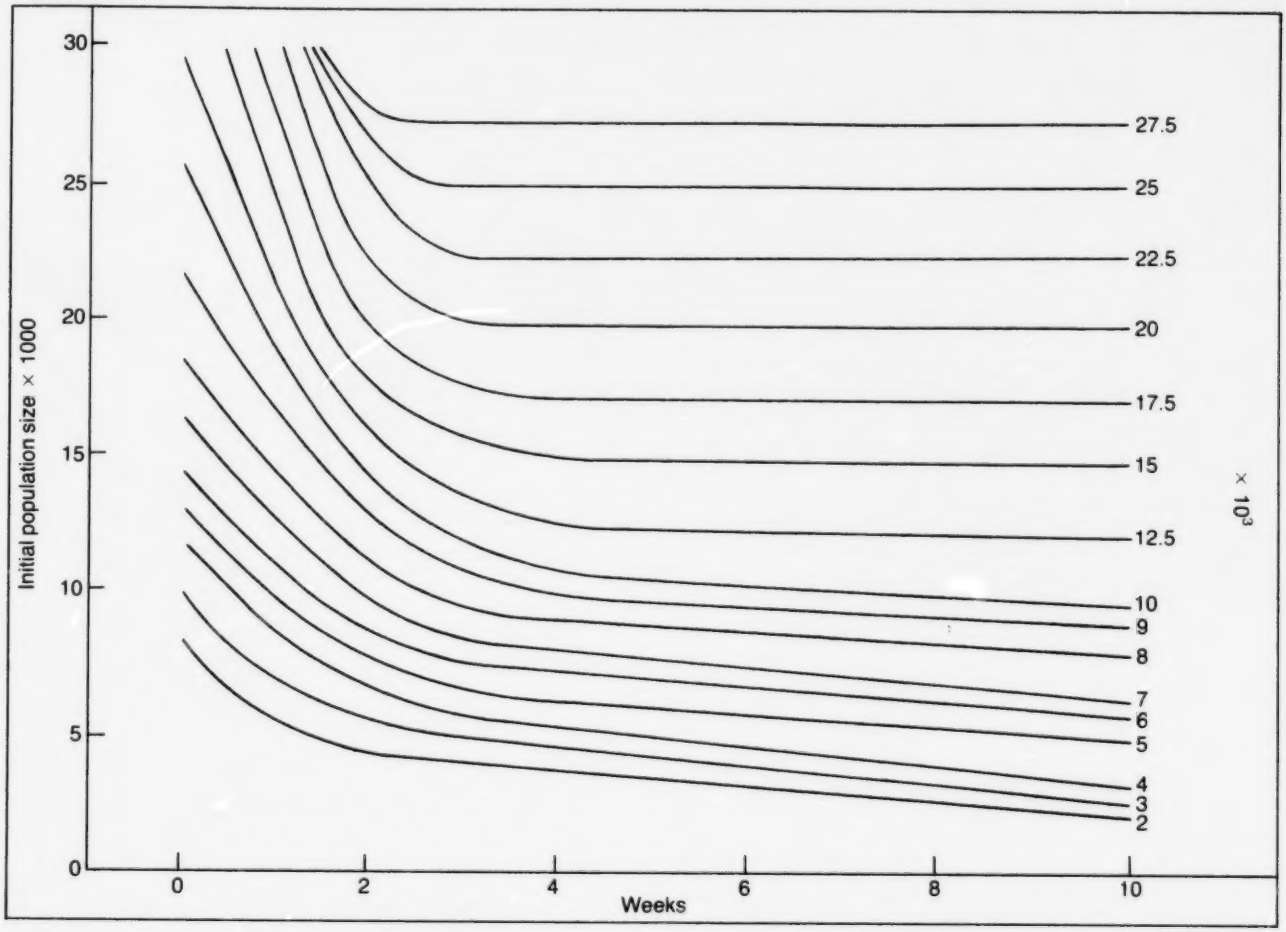
Ducks, geese, and swans, the Anatidae, are a major natural resource of North America. The ducks, Anatinae, are the most numerous, estimates of their numbers have ranged from 35 to 140 million during the past four decades. Twenty-seven species of ducks occur in Canada, the US, and Mexico. Their major breeding grounds are in Canada, some nesting in the far north. Most winter in the southern US and Mexico, although some reach Cuba, Central, and South America. They move between north and south in massive spring and fall migrations. It is on the many stopping or staging areas along migration routes that hunting takes place.

Some members of the Anatinae are hunted in all of Canada and the US and in many parts of Mexico. Hunting begins as early as 1 September in Canada followed by successive opening-of-shooting dates and staggered shooting seasons until all legal gunning ends in February on the southern wintering grounds. Thus some populations including dabbling ducks, such as the Mallard, and diving ducks, such as Lesser Scaup, are subject to gunning during 5 consecutive months. Bellrose (1976) estimated the hunting kill in North America in the early 1970s at 20 million annually.

The Mallard is probably the most abundant duck in the world, although populations have declined recently on some breeding ranges of North America. The Canvasback, once common on prairie marshes, has become rarer over the past 25 years. The Lesser Scaup remains one of the most plentiful game ducks; its extensive breeding range includes prairie, parkland, and boreal forest. The total duck population has decreased during the past 25 years, perhaps due to increased hunting pressure and deteriorating habitat (Hochbaum and Caswell 1978).

Throughout North America, federal governments set waterfowl hunting regulations although in the US states define their own patterns of control within the overall framework. All these countries attempt to control the harvest by restricting the daily bag and the season length, and by

Figure 8
Isopleth diagram showing the relationship between regions of Canvasback kill and population size and season length under normal effort levels observed at Delta



varying opening dates. These methods have been used for some 65 years. At first, each country set the same bag limits for all species. As species such as Canvasback and Redhead declined, managers began to reduce the bag limit or to close the season for those species. Managers allowed larger bags for more plentiful species, such as Lesser Scaup. This type of species-specific regulation assumed that the hunter could identify all species in all plumages despite the fact that visibility was often hampered by low light and bad weather and by the hunters' need for concealment.

Waterfowl managers generally assume that bag limits and season length can be used to manage the harvest and that they should be based on population parameters such as stock size (Bellrose 1950; Geis 1959, 1963; Geis *et al.* 1969; Nagel and Low 1971; Rogers *et al.* 1979; and Patterson 1979). As a result, regulations vary annually, regionally, and specifically according to population data gathered from the breeding grounds each year. These population figures derived from aerial and on-the-ground surveys may vary according to the experience and training of survey members, and are subject to many adjustments for visibility, group sizes, and completeness of search. To complicate matters, managers must set regulations well in advance of the hunting season because of the lengths of administrative procedures required to convert proposals into authorized documents.

Despite the intensity of annual duck surveys and the complexity of the regulatory problem, the effect of variable regulations on survival has been studied extensively only for the Mallard (Anderson and Burnham 1976, 1978; Rogers *et al.* 1979). Furthermore, there have been no studies of the effectiveness of regulations or of the complex interactions between ducks and hunters. The latter must annually memorize new laws covering many species. In the field the hunter is confronted repeatedly by the requirement to make split-second decisions regarding the legality of each encounter with ducks. As many as 10 or 12 different species may come to his or her decoys in a given day.

Our study suggests that complex regulations do not effectively control the kill at least in the absence of intensive enforcement. We found that hunters do not shoot selectively. For instance, even when regulations limit Canvasback kill, the average hunter shoots at all ducks regardless of species. Therefore species-variable bag limits on one shooting area may not be effective. A species, such as Canvasback, is not protected by stipulating a one-bird bag limit for it while larger bag limits are allowed for other species using the same marsh. In the same vein, regulations aimed at increasing the take of a species, as have been used for the Lesser Scaup and some others in the US, may jeopardize protected species (Hickey 1955).

Furthermore, we observed from our spy blind that each species responds differently to hunter effort. If Canvasback are present on a marsh where hunters seek Mallards (with higher bag allowances), the kill of Canvasback can be greater than of Mallard, because of the lesser wariness and greater vulnerability of Canvasback.

Canvasback kill is clearly correlated with local population size. The only manner by which Canvasback harvest may be controlled is by prohibiting all duck hunting in an area when this species is present. In Manitoba this would involve the temporary closure of only a few hunting areas that are traditional Canvasback staging areas.

Our management scenarios also demonstrate some of the not-so-obvious relationships between gunners and mixed stocks. Mallard kill, for instance, remains high in late autumn when hunter effort is reduced. Wariness is not maintained throughout the hunting season. For Lesser Scaup, the kill may increase under reduced pressure. Both species seek to avoid heavy gunning early in the season, but evasiveness declines as encounters with hunters become less frequent. Clearly this does not apply with Canvasback.

Our analysis of the kill data, spy blind observations, and decoy trials indicate that waterfowl harvests are influenced more by bird behaviour and abundance than by current regulations. These studies also reveal that hunter behaviour is little known and requires further investigation.

We conclude that, because of species-specific differences and because of hunter behaviour and its effect on harvest, regulations should be simplified. Our findings suggest that local areas should be closed to all duck hunting when a species requiring protection is in residence. Finally, we contend that regional harvests can be forecast by using multivariate analysis and predictive equations. A predator–prey simulation model such as [7] could be useful for analysis toward effective regulatory action. The use of models may be practicable in the future because management schemes will need to become more refined if increased numbers of hunters are pursuing stable or reduced duck numbers. The effects of more sophisticated management programs will not be obvious and may be analysed using simulation techniques prior to being introduced.

Summary and conclusions

1. We developed a conceptual duck–hunter model and formulated several hypotheses and predictions based on causal relationships among model components and tested them in the field in Manitoba.

2. Vulnerability, an important determinant of kill, was a function of instantaneous hunter effort, not of cumulative experiences with hunters.

3. Mallard were most wary, whereas Lesser Scaup and Canvasback proved to be most vulnerable.

4. Kill patterns were not linearly proportional to population size indicating a non-random encounter process.

5. Handling time did not limit achieved kill per hunter.

6. Time between encounters was independent of duck abundance suggesting that for each encounter there is a period during which birds will not respond to decoys which may have resulted in the non-linear (saturating) kill patterns observed.

7. Hunter effort was correlated to time of season and duck numbers; however, duck numbers may have less to do with effort than the fact that hunters simply lose interest as the season passes and winter approaches.

8. We found no correlation between weather variables and vulnerability.

9. Hunters were not selective in their shooting although small ducks were fired upon less frequently than large ducks.

10. Northern Manitoba Mallard populations, consisting primarily of juveniles, were six times as vulnerable as aggregations mainly of adults at Delta in southern Manitoba.

11. Crippling losses were higher on the Delta Marsh than those reported elsewhere in North America.

12. Distribution patterns of ducks were non-random with clumping in refuges at Delta during the 1973 hunting season.

13. We developed a multi-species simulation model to assess implications of season length, effort, and population size on the kill of Mallard, Canvasback, and Lesser Scaup.

14. We recommend season length manipulations for reducing kill of Mallard; Lesser Scaup survival does not change when hunter effort increases and requires no special regulations. Canvasback kills were large under all circumstances except when duck numbers were small. We recommend shortening seasons to control Canvasback harvests.

15. We suggest using a logarithmic regression model to forecast kill levels and the multi-species simulation model to evaluate management options.

Literature cited

Alford, J.R.; Bolen, E.G. 1977. Differential responses of male and female Pintail ducks to decoys. J. Wildl. Manage. 41(4):657–661.

Anderson, D.R. 1975. A population in a Markovian environment. A theory and example. Ecology 56(6):1281–1296.

Anderson, D.R.; Burnham, K.P. 1976. Population ecology of the Mallard: VI. The effect of exploitation on survival. U.S. Fish Wildl. Serv. Resour. Publ. 128. 66 p.

Anderson, D.R.; Burnham, K.P. 1978. Effect of restrictive and liberal hunting regulations on annual survival rates of the Mallard in North America. North Am. Wildl. Nat. Resour. Conf. Trans. 43:181–186.

Bailey, R.O.; Batt, B.D.J. 1974. Hierarchy of waterfowl feeding with Whistling Swans. Auk. 91(3):488–493.

Bellrose, F.C., Jr. 1944. Waterfowl hunting in Illinois: its status and problems. Nat. Hist. Surv. Biol. Notes No. 17. 33 p.

Bellrose, F.C. 1950. Mississippi Flyway: Problems, projects, prospects. North Am. Wildl. Conf. Trans. 15:123–132.

Bellrose, F.C. 1953. A preliminary evaluation of cripple losses in waterfowl. North Am. Wildl. Conf. Trans. 18:337–360.

Bellrose, F.C. 1976. Ducks, geese, and swans of North America. Stackpole. Harrisburg, Pa. 543 p.

Bellrose, F.C.; Scott, I.G.; Hawkins, A.S.; Low, J.B. 1961. Sex ratios and age ratios in North American ducks. Ill. Nat. Hist. Surv. Vol. 27, Artic. 6. 474 p.

Bergerud, A.T.; Manuel, F.; Whalen, H. 1968. The harvest reduction of a moose population in Newfoundland. J. Wildl. Manage. 32(4):722–728.

Beverton, R.J.H.; Holt, S.J. 1957. On the dynamics of exploited fish populations. Her Majesty's Stationery Off. London. 533 p.

Boyd, H. 1971. Observations on duck hunting in eastern Canada in 1968 and 1969. Can. Wildl. Serv. Occas. Pap. No. 12. 22 p.

Brown, G.M., Jr.; Hammack, J.; Tillman, M.F. 1976. Mallard population dynamics and management models. J. Wildl. Manage. 40(3):542–555.

Charnov, E.L. 1973. Optimal foraging: some theoretical explorations. Ph.D. Thesis. Univ. Washington. 95 p.

Christisen, P.M. 1971. Importance of daily bag in squirrel hunting. North Am. Wildl. Conf. Trans. 36:322–329.

Cowardin, L.M.; Johnson, D.H. 1979. Mathematics and Mallard management. J. Wildl. Manage. 43(1):18–35.

Evard, J.O. 1970. Assessing and improving the ability of hunters to identify flying waterfowl. J. Wildl. Manage. 34(1):114–126.

Geis, A.D. 1959. Annual and shooting mortality estimates for the Canvasback. J. Wildl. Manage. 23(3):253–261.

Geis, A.D. 1963. Regulations in migratory bird management. North Am. Wildl. Conf. Trans. 28:164–171.

Geis, A.D.; Crissey, W.F. 1973. 1970 test of the point system for regulating duck harvests. Wildl. Soc. Bull. 1(1):1–21.

Geis, A.D.; Martinson, R.K.; Anderson, D.R. 1969. Establishing hunting regulations and allowable harvest of Mallards in the United States. J. Wildl. Manage. 33(4):848–859.

Hickey, J.J. 1955. Is there a scientific basis for flyway management? North Am. Wildl. Conf. Trans. 30:126–150.

Hochbaum, G.S.; Caldwell, P.J. 1977. The 1973 kill of Canvasback under restrictive hunting regulations, Delta Marsh, Manitoba. Can. Wildl. Serv. Prog. Note No 76. 6 p.

Hochbaum, G.S.; Caswell, F.D. 1978. A forecast of long-term trends in breeding Mallard populations on the Canadian prairies. Can. Wildl. Serv. Prog. Note No. 90. 8 p.

Hochbaum, H.A. 1955. Travels and traditions of waterfowl. Univ. Minnesota Press. 301 p.

Hochbaum, H.A.; Dillon, S.T.; Howard, J.L. 1954. An experiment in the control of waterfowl depredation. North Am. Wildl. Conf. Trans. 19:176–185.

Holling, C.S. 1959*a*. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91:385–398.

Holling, C.S. 1959*b*. The components of predation as revealed by a study of small mammal predation on the European Pine Sawfly. Can. Entomol. 91:293–320.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. No. 48. 1–86.

Kirby, R.E.; Riechmann, J.H., Shough, M.E. 1976. A preliminary report on Minnesota's innovative 1973 waterfowl season. Wildl. Soc. Bull 4(2):55–63.

Koerner, J.W.; Bookhout, T.A.; Bednarik, K.E. 1974. Movements of Canada Geese color-marked near southwestern Lake Erie. J. Wildl. Manage. 38(2):275–289.

Leopold, A. 1933. Game management. Charles Scribner and Sons. N.Y. 481 p.

McKinney, D.F. 1975. The evolution of duck display. Pages 331–357 *in* Baerends, G.; Beer, C.; Manning, A. ed. Function and evolution in behaviour. Clarendon Press. Oxford.

Melzack, R. 1961. On the survival of Mallard ducks after "habituation" to the hawk-shaped figure. Behaviour 17:9–16.

Nagel, J.E.; Low, J.B. 1971. Effect of regulations on waterfowl kill in Utah. J. Wildl. Manage. 35(3):554–557.

Olson, D.P. 1965. Differential vulnerability of male and female Canvasbacks to hunting. North Am. Wildl. Conf. Trans. 30:121–135.

Patterson, J.H. 1979. Can ducks be managed by regulation? Experiences in Canada. North Am. Wildl. Nat. Resour. Conf. Trans. 44:130–139.

Powell, G.V.N. 1974. Experimental analysis of social value of flocking by Starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav. 22(2):501–505.

Ricker, W.E. 1958. Maximum sustained yield from fluctuating environments and mixed stocks. J. Fish. Res. Board Canada. 15:991–1006.

Rogers, J.P.; Nichols, J.D.; Martin, F.W.; Kimball, C.F.; Pospahala, R.S. 1979. Can ducks be managed by regulation? An examination of harvest and survival rates of ducks in relation to hunting. North Am. Wildl. Nat. Resour. Conf. Trans. 44:114–126.

Roseberry, J.L.; Klimstra, W.D. 1974. Differential vulnerability during a controlled deer harvest. J. Wildl. Manage. 38(3):499–507.

Royama, T. 1970. Evolutionary significance of predator's response to local differences in prey density: A theoretical study. Pages 344–357 *in* denBoer, P.J.; Gradwell, G.R. Proc. Adv. Study Inst. Dyn. Numbers Popul. Oosterbeek.

Siegfried, W.R.; Underhill, L.G. 1975. Flocking as an anti-predator strategy in doves. Anim. Behav. 23:504–508.

Sowls, L.K. 1955. Prairie ducks. Stackpole. Harrisburg, Pa. 193 p.

Stott, R.S.; Olson, D.P. 1972. Differential vulnerability patterns among three species of sea ducks. J. Wildl. Manage. 36(3):775–783.

Teplov, V.F.; Kartashev, N.N. 1957. Wildfowl research in Russia. Wildfowl Trust. 9:157–169.

Thorpe, W.H. 1963. Learning and instinct in animals. Methuen. London. 558 p.

Walters, C.J.; Reed, R.; Ward, J. 1973. Some factors determining success of duck hunters in southern British Columbia. Can. Wildl. Serv. Prog. Note No. 36. 6 p.

Walters, C.J.; Hilborn, R.; Oguss, E.; Peterman, R.M.; Stander, J.M. 1974. Development of a simulation model of Mallard duck populations. Can. Wildl. Serv. Occas. Pap. No. 20. 35 p.

Other publications in the Occasional Papers Series

No. 1
Birds protected in Canada under the Migratory Birds Convention Act, 4th ed. Publication bilingue.
Cat. No. CW69-1/1. Publ. 1957, rev. 1980.

No. 2
Canadian bird names, French, English and scientific.
Publication bilingue.
Cat. No. CW69-1/2. Publ. 1957, rev. 1972.

No. 3
Use of aerial surveys by the Canadian Wildlife Service by D.A. Benson.
Out of print.
Cat. No. CW69-1/3. Publ. 1963, repr. 1966.

No. 4
Queen Elizabeth Islands game survey, 1961 by J.S. Tener.
Cat. No. CW69-1/4. Publ. 1963, repr. 1972.

No. 5
Age determination in the polar bears by T.H. Manning.
Cat. No. CW69-1/5. Publ. 1964, repr. 1973.

No. 6
A wildlife biologist looks at sampling, data processing and computers by D.A. Benson.
Out of print.
Cat. No. R69-1/6. Publ. 1964.

No. 7
Preliminary report on the effects of phosphamidon on bird populations in New Brunswick by C.D. Fowle. Out of print.
Cat. No. R69-1/7. Publ. 1965.

No. 8
Birds of Nova Scotia – New Brunswick border region by G.F. Boyer.
Cat. No. CW69-1/8. Publ. 1966, repr. 1981.

No. 9
Effects of dietary methylmercury on Ring-necked Pheasants, with special reference to reproduction by N. Fimreite.
Cat. No. R69-1/9. Publ. 1971.

No. 10
Trends in populations of barren-ground caribou over the last two decades: a re-evaluation of the evidence by G.R. Parker.
Cat. No. CW69-1/10. Publ. 1971, repr. 1972.

No. 11
The Canada migratory game bird hunting permit and related surveys by D.A. Benson.
Cat. No. R69-1/11. Publ. 1971.

No. 12
Observations on duck hunting in eastern Canada in 1968 and 1969 by J.H. Boyd.
Cat. No. R69-1/12. Publ. 1971.

No. 13
Evaluation of ecological effects of recent low water levels in the Peace–Athabasca Delta by H.J. Dirschl.
Cat. No. CW69-1/13. Publ. 1972.

No. 14
The Great Cormorants of eastern Canada by A.J. Erskine.
Cat. No. CW69-1/14. Publ. 1972.

No. 15
Distribution of barren-ground caribou harvest in north-central Canada by G.R. Parker.
Cat. No. CW69-1/15. Publ. 1972.

No. 16
Bird migration forecasts for military air operations by H. Blokpoel.
Cat. No. CW69-1/16. Publ. 1973.

No. 17
Waterfowl populations on the Peace–Athabasca Delta. 1969 and 1970 by D.J. Nieman and H.J. Dirschl.
Cat. No. CW69-1/17. Publ. 1973.

No. 18
Gammarus predation and the possible effects of *Gammarus* and *Chaoborus* feeding on the zooplankton composition in some small lakes and ponds in western Canada by R.S. Anderson and L.G. Raasveldt.
Cat. No. CW69-1/18. Publ. 1974.

No. 19
A summary of DDE and PCB determinations in Canadian birds, 1969 to 1972 by M. Gilbertson and L. Reynolds.
Cat. No. CW69-1/19. Publ. 1974.
No. 20
Development of a simulation model of Mallard Duck populations by C.J. Walters, R. Hilborn, E. Oguss, R.M. Peterman and J.M. Stander.
Cat. No. CW69-1/20. Publ. 1974.
No. 21
Use of museum specimens in toxic chemical research by A.M. Rick.
Cat. No. CW69-1/21. Publ. 1975.
No. 22
Impoundments for waterfowl by W.R. Whitman.
Cat. No. CW69-1/22. Publ. 1976.
No. 23
Minimizing the dangers of nesting studies to raptors and other sensitive species by R.W. Fyfe and R.R. Olendorff.
Cat. No. CW69-1/23. Publ. 1976.
No. 24
Waterfowl damage to Canadian grain: current problems and research needs by L.G. Sugden.
Cat. No. CW69-1/24. Publ. 1976.
No. 25
Census techniques for seabirds of arctic and eastern Canada by D.N. Nettleship.
Cat. No. CW69-1/25. Publ. 1976.
No. 26
Notes on the present status of the polar bear in James Bay and Belcher Islands area by Charles Jonkel, Pauline Smith, Ian Stirling and George B. Kolenosky.
Cat. No. CW69-1/26. Publ. 1976.
No. 27
Limnological and planktonic studies in the Waterton Lakes, Alberta by R. Stewart Anderson and Roderick B. Green.
Cat. No. CW69-1/27. Publ. 1976.
No. 28
Birds and mammals of the Belcher, Sleeper, Ottawa, and King George Islands, Northwest Territories by T.H. Manning.
Cat. No. CW69-1/28. Publ. 1976.
No. 29
Developments in PPS sampling – Impact on current research by A.R. Sen.
Cat. No. CW69-1/29. Publ. 1976.
No. 30
Dynamics of snowshoe hare populations in the Maritime Provinces by Thomas J. Wood and Stanley A. Munroe.
Cat. No. CW69-1/30. Publ. 1977.
No. 31
Migration and population dynamics of the Peace–Athabasca Delta goldeye population by D.B. Donald and A.H. Kooyman.
Cat. No. CW69-1/31. Publ. 1977.
No. 32
The effects of fire on the ecology of the Boreal Forest, with particular reference to the Canadian north; a review and selected bibliography by John P. Kelsall, E.S. Telfer and Thomas D. Wright.
Cat. No. CW69-1/32. Publ. 1977.
No. 33
The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay by Ian Stirling, Charles Jonkel, Pauline Smith, Richard Robertson and Dale Cross.
Cat. No. CW69-1/33. Publ. 1977.
No. 34
Canvasback habitat use and production in Saskatchewan parklands by Lawson G. Sugden.
Cat. No. CW69-1/34. Publ. 1978.
No. 35
The diets of muskoxen and Peary caribou on some islands of the Canadian High Arctic by Gerald R. Parker.
Cat. No. CW69-1/35. Publ. 1978.
No. 36
Observations of Mallards in the parkland of Alberta by Michael F. Sorensen.
Cat. No. CW69-1/36. Publ. 1978.
No. 37
The wildlife valuation problem: A critical review of economic approaches by William A. Langford and Donald J. Cocheba.
Cat. No. CW69-1/37. Publ. 1978.
No. 38
Spatial changes in waterfowl habitat, 1964-74, on two land types in the Manitoba Newdale Plain by G.D. Adams and G.G. Gentle.
Cat. No. CW69-1/38. Publ. 1978.
No. 39
Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories, in August and September 1976 by D.N. Nettleship and A.J. Gaston.
Cat. No. CW69-1/39. Publ. 1978.
No. 40
Responses of Peary caribou and muskoxen to helicopter harassment by Frank L. Miller and Anne Gunn.
Cat. No. CW69-1/40. Publ. 1979.
No. 41
Avian Community structure of six forest stands in La Mauricie National Park, Quebec by J.-L. DesGranges. Disponible également en français.
Cat. No. CW69-1/41E. Publ. 1979.
No. 42
Population ecology studies of the polar bear in northern Labrador by Ian Stirling and H.P.L. Kiliaan. Disponible également en français.
Cat. No. CW69-1/42E. Publ. 1980.
No. 43
Census methods for murres, *Uria* species; a unified approach by T.R. Birkhead and D.N. Nettleship. Disponible également en français.
Cat. No. CW69-1/43E. Publ. 1980.
No. 44
Population ecology studies of the polar bear in the area of southeastern Baffin Island by Ian Stirling, Wendy Calvert, and Dennis Andriashek. Disponible également en français.
Cat. No. CW69-1/44E. Publ. 1980.
No. 45
Polynyas in the Canadian Arctic by Ian Stirling and Holly Cleator, eds. Disponible également en français.
Cat. No. CW69-1/45E. Publ. 1981.
No. 46
The Lesser Snow Geese of the eastern Canadian Arctic by H. Boyd, G.E.J. Smith, and F.G. Cooch. Disponible également en français.
Cat. No. CW69-1/46E. Publ. 1982.
No. 47
The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79 by Ian Stirling, Michael Kingsley, and Wendy Calvert. Disponible également en français.
Cat. No. CW69-1/47E. Publ. 1982.
No. 48
Foraging behaviour of Peary caribou in response to springtime snow and ice conditions by F.L. Miller, E.J. Edmonds, and A. Gunn. Disponible également en français.
Cat. No. CW69-1/48E. Publ. 1982.
No. 49
A review of some important techniques in sampling wildlife by A.R. Sen. Disponible également en français.
Cat. No. CW69-1/49E. Publ. 1982.
No. 50
Intensive regulation of duck hunting in North America: its purpose and achievements by Hugh Boyd. Disponible également en français.
Cat. No. CW69-1/50E. Publ. 1983.
No. 51
Human dimensions of migratory game-bird hunting in Canada by Shane A.D. Parker and Fern L. Filion. Disponible également en français.
Cat. No. CW69-1/51E. Publ. 1984.